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A new species of *Rattus* (Rodentia: Muridae) from Manus Island, Papua New Guinea

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We describe a new species of *Rattus*, from 3 modern specimens collected on Manus Island in the Admiralty Group, Papua New Guinea, between 2002 and 2012. Subfossil specimens of early to late Holocene age from the Pamwak archaeological site on Manus Island are referred to the new species on morphological criteria; these confirm the species as a long-term resident of Manus Island. The new species is distinguished by its combination of large size; short tail; dorsal pelage that is coarse, spiny, and dark, with prominent black guard hairs; and sharply contrasting cream ventral pelage. Based on its overall body form, the species is almost certainly terrestrial. The dentition combines robust incisors with relatively small molars and the cranium displays a distinctive mélange of characters—including an elongate and anteriorly expanded rostrum and a mesopterygoid fossa that is narrow anteriorly and broadens to the rear. Sequence data from the mitochondrial *control region* and 3 nuclear genes place the new species as a highly divergent member of the Australo–Papuan *Rattus* radiation, with no identified close relative among sampled taxa. Morphological comparisons are made between the new species and other pertinent species of *Rattus* from the region, including *R. sanila*, a species known only from Late Pleistocene fossil to Late Holocene subfossil remains from an archaeological site on New Ireland. The conservation status of the new species is discussed in the light of a recent survey that failed to locate surviving populations in 2 areas of natural forest on Manus Island. Further survey work is urgently needed to identify any surviving populations and to assess the role of potential threats to the species.

Key words: Admiralty Islands, Australo–Papuan Region, biogeography, Bismarck Archipelago, conservation, mitochondrial control region, molecular phylogeny, morphology, nuclear genes, *Rattus sanila*

The rodent genus *Rattus* Fischer, 1803, currently comprises 67 recognized species (Musser and Carleton 2005; Maryanto et al. 2010), of which 3 appear to have become extinct in historical times. The genus shows its greatest disparity on mainland Asia and almost certainly arose there (Pagès et al. 2011; Fabre et al. 2013). However, the highest species diversity is present in insular Southeast Asia, Melanesia, and in Australia, each of which supports rich local radiations (Musser and Heaney 1985; Musser and Holden 1991; Rowe et al. 2011). Melanesia, which comprises the island of New Guinea and its satellites, has 17 native species currently recorded (Flannery 1995a, 1995b; Musser and Carleton 2005; Maryanto et al. 2010), though a recent genetic survey points to additional cryptic diversity, especially among the small montane species (Robins et al. 2014). Most Melanesian islands also support populations of 2 or more introduced species of *Rattus* that have spread as commensals of humans in prehistoric to colonial times (Flannery 1995b; Matisoo-Smith and Robins 2004; Aplin et al. 2011).

Here we describe a new species of *Rattus* from Manus Island in the Admiralty Group, Bismarck Archipelago, Papua New Guinea, based on 3 specimens, 2 obtained in 2002 and 1 in 2012. We also refer subfossil specimens of *Rattus* from an Early to Mid-Holocene archaeological site on Manus Island to the new species, thereby confirming the new species as a long-term resident of the island.

The Admiralty Group lies about 2 degrees south of the equator and some 275–300 km north of the island of New Guinea. It comprises 18 islands with a total land area of 2,100 km^2. Manus is the largest island of the group (approximately 1,900 km^2) and reaches a maximum elevation of 720 m on Mt. Dremsel. The islands arose along a volcanic arc during the mid-Tertiary to late Tertiary (Davies 2012) and were not connected to New Guinea or any other landmass during Quaternary glacial cycles (Voris 2000). Mussau Island in the St. Matthias Group lies some 260 km to the east, while Lavongai Island (formerly New Hanover; located northwest of New Ireland) and New Britain are 300 km and 390 km away, to the east and southeast, respectively. The dominant natural vegetation of the Admiralty Group is primary evergreen forest, including tropical and subtropical moist broadleaf forests (Wikramanayake et al. 2002). On floristic criteria, these communities have been identified as being of high regional biological significance (Johns 1993; Wikramanayake et al. 2002).

Prior to the collection of the new *Rattus* species, only 4 species of rodents were recorded in the modern fauna of the Admiralty Group. Taylor et al. (1982) reported *R. praetor* (Thomas, 1888) from Bat Island, which lies approximately 70 km southwest of Manus Island, and identified museum specimens of 2 species of *Rattus* from the Admiralty Group, with both occurring on Manus—*R. exulans* (Peale, 1848) [see also (Thomas 1914]) and *R. rattus* (Linnaeus, 1758). Both are widespread commensals of humans. The 4th species was collected in 1988 on Manus Island, the endemic Manus Melomys *Melomys matambuai* Flannery, Colgan, and Trimble, 1994. Two other species of rodents listed for Manus by Menzies and Dennis (1979)—*Rattus ruber* (Jentink, 1879) [= *R. praetor*], followed by Flannery (1995b), and *Uromys neobrittanicus* Tate and Archbold, 1935—are unsubstantiated to our knowledge, either by literature references or by vouchers. In their discussion of *M. matambuai*, Musser and Carleton (2005:1379), in an apparent lapsus, erroneously gave the range of *M. bougainville* Troughton, 1936, as "Manus Isl."

Archaeological samples from Manus Island have been cited as evidence of a formerly more diverse rodent fauna. Williams (1997, 1999) reported examples of *R. mordax* (Thomas, 1904a), cf. *R. mordax*, *R. praetor*, *R. rattus*, and *Rattus* sp., but not *R. exulans*, in a large assemblage of latest Pleistocene fossils and remains of more recent age, from the Pamwak archaeological site (see Fredericksen et al. 1993 for site details). White et al. (2000) mentioned Williams's (1997, 1999) determinations in their review of the historical and present distribution of the semicommensal *R. praetor.* However, Flannery (1995b:38) had earlier reexamined the Pamwak rodents and found only *M. matambuai* and a "large species of *Rattus*, probably representing an undescribed species, (that) persists into the most recent levels." Flannery's assessment was confirmed by Aplin who restudied the Pamwak rodent assemblage as part of the present study.

In August 2002, Ann Williams, working on a biotic survey of Manus for Conservation International, obtained 2 specimens of a large *Rattus*—a nearly complete skeleton and an isolated mandible—from hunters at the village of Tulu No. 1 along the northwestern coast. A full decade later, in August 2012, Weijola obtained a complete adult female specimen of the same large, distinctive species while conducting fieldwork on monitor lizards in the central hill forests of Manus Island.

Here we 1) describe the new species of *Rattus* from Manus Island, based on the available modern and archaeological specimens; 2) assess the distinctiveness of this species in comparison with other *Rattus* in the region, using molecular genetic and morphological data; 3) relate our new observations to current views regarding the biogeography of Australo–Papuan *Rattus* and of the Admiralty Group; and 4) discuss the conservation status of the new species.

Materials and Methods

Taxon sampling.—Taxonomic assessment of the Manus *Rattus* was aided by the extensive morphological reviews of Australian and Melanesian *Rattus* by Taylor and coworkers (Taylor and Horner 1973; Taylor et al. 1982) and by subsequent work in the field (Flannery 1995a, 1995b) and in collections (Musser and Carleton 2005). Taylor et al. (1982) included a critical assessment of all of the available names applied to Melanesian *Rattus*. We follow their assessments of synonymy. For the molecular genetic study, we compared sequences obtained for the new species, with all available data from Australo–Papuan *Rattus* (Robins et al. 2010, 2014; Rowe et al. 2011) and from a range of other *Rattus* species representing other geographic radiations. Three of the currently recognized extant species of *Rattus* in Melanesia are unrepresented in the genetic taxon sampling—*R. jobiensis* Rümmler, 1935; *R. omichlodes* (Misonne, 1979); and *R. richardsoni* (Tate, 1949). Also missing from our sampling is the Gag Island population described recently as a new species—*R. nikenii* Maryanto et al., 2010—but which in our view may be an insular variant of *R. steini*. Of these, only *R. jobiensis* is a serious candidate for identity with the Manus rat, as *R. omichlodes* and *R. richardsoni* are both small species of subalpine habitats of the central ranges of New Guinea.

Morphological techniques.—Craniodental measurements were taken with dial calipers; the majority of mensural points follow Taylor et al. (1982) to facilitate comparison with their tables of measurements. Percentages given of head + body length, as compared to total length, in species other than the new *Rattus* from Manus are calculated from figures given in tables by Taylor et al. (1982). Descriptive terminology for the skull and teeth follows that used in many publications on murine rodents by Musser (e.g., Musser 1982; Musser and Lunde 2009). Upper and lower molars are designated by "M" and "m," and upper and lower incisors are designated by "I" and "i," respectively. Length of hind foot does not include claw.

Specimens from the following institutions (acronyms in parentheses) are used for comparisons: Australian Museum (AMS), Sydney, New South Wales; Australian Biological Tissue Collection (ABTC), South Australian Museum (SAM), Adelaide, South Australia; National Museum & Art Gallery, Port Moresby, Papua New Guinea (PNGMAG); American Museum of Natural History (AMNH), New York; Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii; Field Museum (FMNH), Chicago, Illinois; Natural History Museum of Los Angeles County (LACM), Los Angeles, California; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; University of Kansas Natural History Museum (KU), Lawrence, Kansas; and University of Wisconsin Zoological Museum (UWZM), Madison, Wisconsin. Specimens used in craniodental comparisons are listed in Supporting Information S1.

The archaeological specimens were compared with the modern specimens, for consistency of dental and bony structures. Whenever possible, measurements of molar lengths and widths and incisor widths and depths were taken. Bivariate plots were examined to identify possible outliers that might indicate the presence in the sample of more than 1 species.

Molecular genetic techniques.—DNA was extracted from tissue samples, using a Puregene DNA Isolation Kit (Gentra Systems, Minneapolis, Minnesota), following the manufacturer's protocol for 5–10 mg of fresh or frozen tissue. The mitochondrial *control region* (*CR*) and 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB* were amplified with the following sets of primers: mt15996L (5′-CTCCACCATCAGCACCCAAAGC-3′) and mt16502H (5′-TTTGATGGCCCTGAAGTAAGAACCA-3′) for the *CR* (Houlden et al. 1999); Atp5A1_F (5′-TTATCCCCCGA ATCTCTGTG-3′) and Atp5A1_R (5′-TGCAAACAAACG GGTTGTAA-3′) for ATP5A1; Fgb_F (5′-GGGGAGAACAGAA CCATGACCATCCAC-3′) and Fgb_R (5′-ACCCCAGTAGTA TCTGCCATTCGGATT-3′) for *FGB*; and DHFR_F (5′-GTCCC AAAATATGGGCATTG-3′) and DHFR_R (5′-TGCCCAG GTTTTTATTCTGG-3′) for *DHFR* (Rowe et al. 2011). PCRs were set up in 25 µL volumes containing a final concentration of 1 Unit Immolase DNA Polymerase (Bioline), 2 × PCR Buffer (Immolase, Bioline), 7.5 mM $MgSO_4$, 1 mM each dNTP, 0.24 µM forward and reverse primers, and 2–3 µL of template DNA. PCRs were performed on an Eppendorf PCR machine (Thermo Fisher Scientific Australia Pty Ltd, Scoresby, Victoria, Australia), according to the following protocol: 95°C for 10 min, 35 cycles at 94°C for 45 s, 60°C for 45 s, 72°C for 1 min, and a final extension of 6 min at 72°C (the annealing temperature of each primer set was optimized independently—57°C for mt15996L/mt16502H and Fgb_F/Fgb_R, 60°C for LM1268/LM1269, and 50°C for Atp5A1_F/Atp5A1_R and DHFR_F/DHFR_R). We included negative controls in all experiments, to monitor contamination. PCR products were separated by electrophoresis on a 1.5% agarose gel. Successful PCR products (20 µL) were purified using Multiscreen PCR cleanup plates (EMD Millipore Corporation, Billerica, Massachusetts). The purified PCRs were sent to the Australian Genome Research Facility for cycle sequencing in both directions, using Big Dye Terminator v3.1 reagents and subsequent capillary sequencing.

We produced new sequences from 2 specimens of *R. mordax* and from the holotype of the new species and aligned our sequences with data from Rowe et al. (2011) for the remaining Australo–Papuan *Rattus* and outgroups, using Geneious version 5.5.6 (Biomatters Limited, Auckland, New Zealand). GenBank accession numbers for all sequences used are presented in Supporting Information S2.

We conducted phylogenetic analyses on the concatenated, mitochondrial, and nuclear alignments, using Bayesian (MrBayes) and maximum likelihood (PhyML) algorithms after use of PartitionFinder version 1.0.1 (Lanfear et al. 2012) to determine the best partitioning strategy and models of nucleotide substitution (HKY for *FGB*, and HKY+G for the *CR*, and *DHFR* and *ATP5A1*). MrBayes v.3.2 (Ronquist et al. 2012) was run using 4 chains for 2.5 million generations, with trees and parameters recorded every 250 generations, and with unlinked parameters for each partition and branch lengths allowed to vary proportionally across partitions. PhyML (Guindon et al. 2009) was used to compute the best maximum likelihood tree using both the Nearest Neighbor Interchange (NNI) algorithm to improve the starting tree and Subtree Pruning and Regrafting (SPR) topological moves to efficiently sample tree space with 3 random starting trees. One hundred bootstrap pseudoreplications were performed on the best tree. RAxML (Stamatakis 2014) was used to compute the best maximum likelihood tree for the extended mtDNA *CR* dataset, using a GTR + gamma model of nucleotide substitution with a rapid bootstrap analysis.

Results

Rattus detentus, new species Timm, Weijola, Aplin, Flannery, and Pine

Admiralties Rat

Figs. 1, 2, 4, 5

Rattus praetor: Williams 1999:244; not *Mus praetor* Thomas, 1888.

Rattus mordax: Williams 1999:244; not *Mus mordax* Thomas, 1904a.

Holotype.—Adult female obtained by Valter Weijola on 24 August 2012. Voucher specimen fixed in formalin, preserved in spirit, and registered as PNGMAG 274363 (and AMS M45608) in the National Museum & Art Gallery, Port Moresby, Papua New Guinea (Figs. 1A, 1C, and 1D). Tissue sample preserved in ethanol and registered as ABTC 125036 in the Australian Biological Tissue Collection, South Australian Museum, Adelaide. Extracted skull is in excellent condition, all teeth fully erupted and moderately worn, cranium with advanced fusion of basicranial synchondroses (Fig. 2).

Type locality.—Vicinity of a small stream near western end of Kawaliap Village, el. 200 m (2°6′40″S, 147°3′40″E), Manus Island, Admiralty Islands, Manus Province, Papua New Guinea.

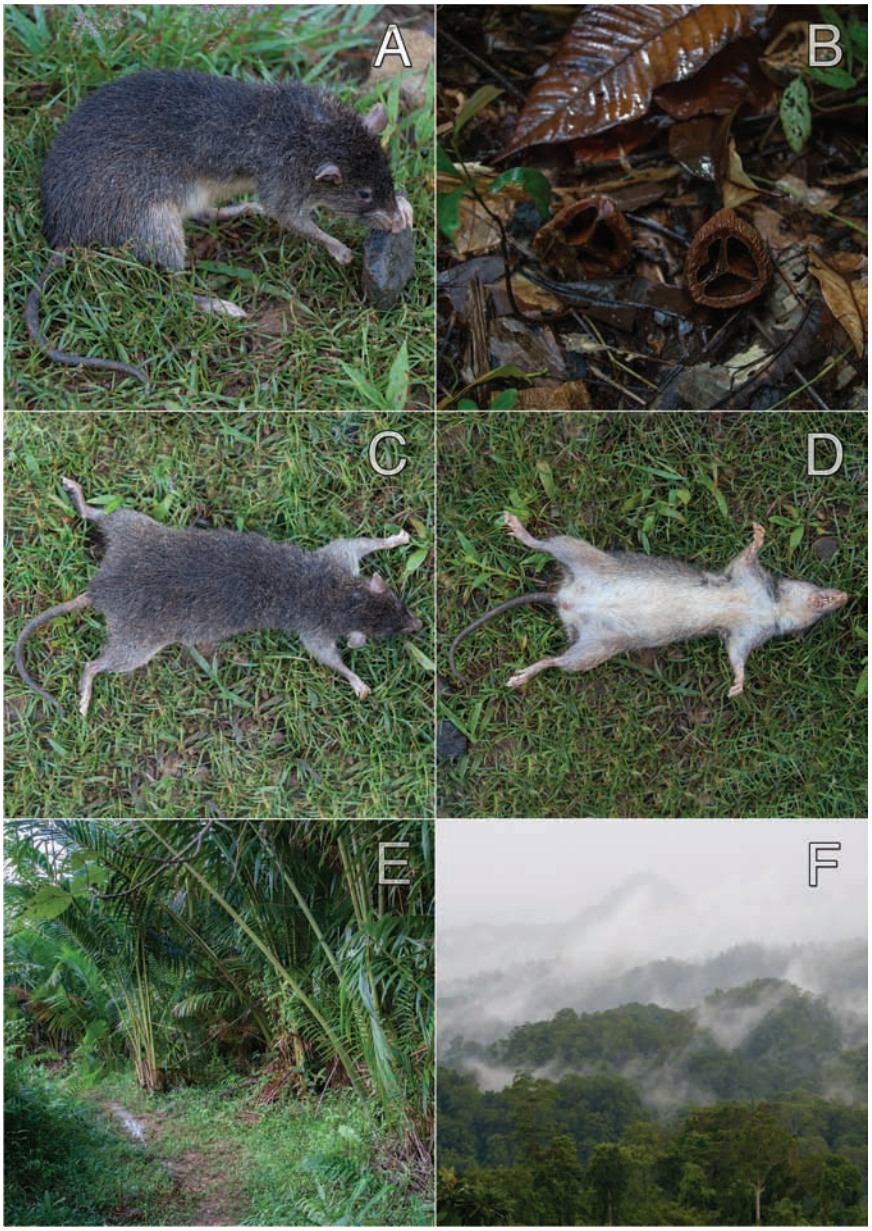

Fig. 1.—A) Adult female *Rattus detentus* (PNGMAG 274363—holotype) from Manus Island. B) Nuts from *Canarium indicum* (Burseraceae) with gnawing marks most likely made by *R. detentus*. C) Adult female *R. detentus* (PNGMAG 274363—holotype), dorsal view. D) Adult female *R. detentus* (PNGMAG 274363—holotype), ventral view. E) Collection site of the *R. detentus* holotype, a traditional subsistence garden and grove of *Metroxylon* near Kawaliap Village. F) Elevated view of the forest where *R. detentus* is found.

Paratypes.—KU 163723: skull and almost complete postcranial skeleton of a young adult of unknown sex. The animal had been killed by local villagers, its carcass buried and the skeleton retrieved and given to Ann Williams on 3 August 2002. All teeth are fully erupted but little worn, and the basicranial synchondroses are not fused (Fig. 2). The skull is missing both jugals and the hamuli of both pterygoids; mandibular rami are separated. KU 163724: mandible only of an adult of unknown sex, dug up from the same hole as KU 163723 and at the same time (Andrew L. Mack, field number 1573). Both specimens were obtained from the villagers at the village of Tulu No. 1, elevation 34 m, Manus Island, Admiralty Islands, Manus Province, Papua New Guinea (01°57′37″S, 146°50′28″E). Associating the correct mandible with the cranium was possible because the 2 individuals are of different ages and sizes.

Referred material.—One hundred and ninety-one subfossil specimens from Pamwak archaeological site, located in the vicinity of Piterait Village, at elevation 30 m, 4 km inland of the south coast of Manus, Admiralty Islands, Manus Province, Papua New Guinea (Fredericksen et al. 1993). The subfossil sample includes 5 dentaries with m1–3; 11 dentaries with 1 or 2 molars retained; 26 examples of m1; 23 examples of m2; 13 examples of m3; 79 examples of the lower incisor; and 34 examples of the upper incisor. The subfossil series is consistent in both morphological and metric attributes with the modern specimens and there is no indication that the

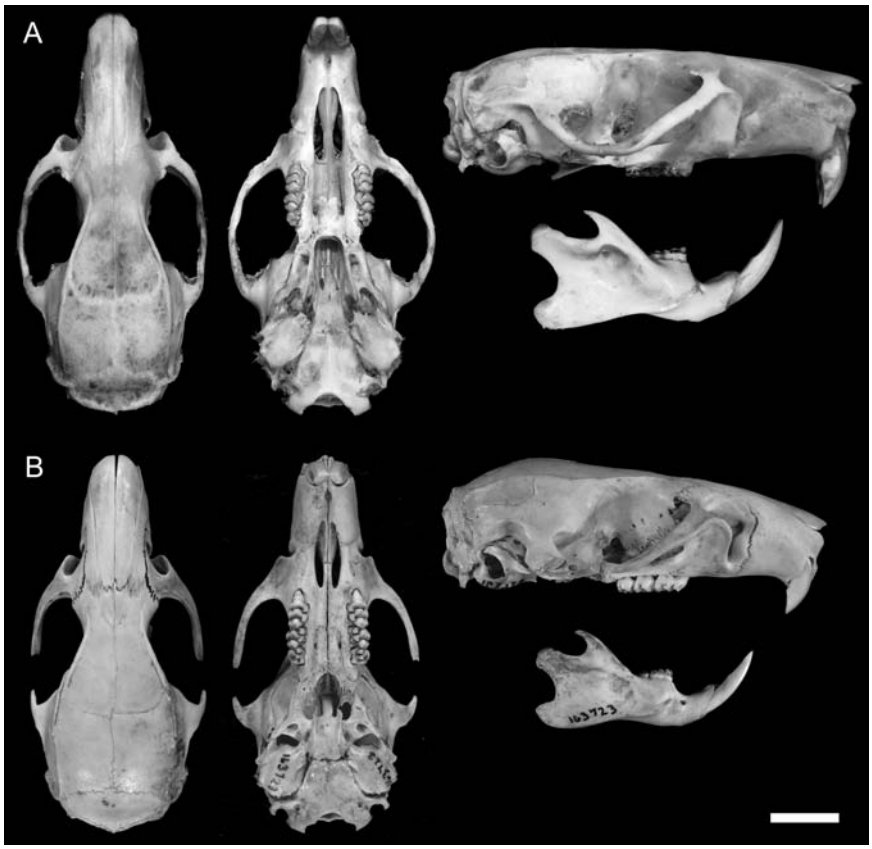

Fig. 2.—Dorsal, ventral, and lateral views of the crania and lateral views of dentaries of adult *Rattus detentus*: A) PNGMAG 274363—holotype; B) KU 163723—a paratype. Scale bar represents 10 mm.

sample contains any additional species. The earliest levels of Pamwak date to approximately 14,000 years ago, but the faunal remains including the *Rattus* specimens are derived from contexts younger than approximately 9,000 years ago. These specimens are the property of the National Museum & Art Gallery, Port Moresby, Papua New Guinea (PNGMAG), and form part of its Archaeology Collection.

Distribution.—Currently known as a living animal from 2 localities on Manus and from subfossil remains from the Pamwak archaeological site (Fig. 3).

Etymology.—detentus (Latin for detained), in reference to the isolation of this Melanesian *Rattus* lineage on Manus Island and to the recent use of the island to detain people seeking political and/or economic asylum in Australia.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new species (*R. detentus*): urn:lsid:zoobank.org:pub:E855E9C8-F224-4B3F-A5E9-47D154DAF06F.

Diagnosis.—A large, short-tailed (approximately 58% of head + body length) species of *Rattus* with mammary formula: 1 pectoral + 1 postaxillary + 2 inguinal. Pelage exceptionally coarse and spiny, with prominent black guard hairs. The animal's size exceeds that attained by all other Melanesian *Rattus* except *R. jobiensis*, and possibly some eastern Melanesian populations of *R. praetor coenorum* Thomas, 1922. Tail at 58% of body length is proportionally shorter than in all other New Guinean *Rattus* species, including the 5 species that approach *R. detentus* in size [i.e., *R. jobiensis* (averaging 92.0% of head + body length), *R. leucopus* (Gray, 1867) (averaging 84.7–89.9% of head + body length in the 3 New Guinean subspecies), *R. mordax* (averaging 83.5% of head + body length in *R. m. mordax* and 82.1% in *R. m. fergussoniensis* Laurie, 1952), *R. praetor* (averaging 78.1% of head + body length in *R. p. praetor* and 89.4% in *R. p. coenorum*), and *R. steini* Rümmler, 1935 (averaging 86.0–101.5% of head + body length in the 4 recognized subspecies)].

Rattus detentus may be distinguished cranially from all other species of *Rattus* by the following combination of characters: rostrum elongate and anteriorly broadened; incisive foramina short, terminating anterior to the molar rows; interorbital region broad; auditory bullae relatively small, weakly inflated; mesopterygoid fossa with narrow, U-shaped anterior margin, then widening posteriorly; pterygoid fossa narrow. Distinguished dentally by combination of relatively small, simple molars (i.e., lacking accessory ridges or posterior cingula on upper molars and accessory cuspids on lower molars) and broad, heavy incisors.

Description.—A large (mass 430 g; head + body length 260 mm), heavily built, terrestrial rat with harsh pelage (Figs. 1A, 1C, 1D, and 4). Dorsum dark gray overall but heavily flecked with pale gray and bearing numerous translucent spines (some with rufous or dark tips) and coarse, conspicuous,

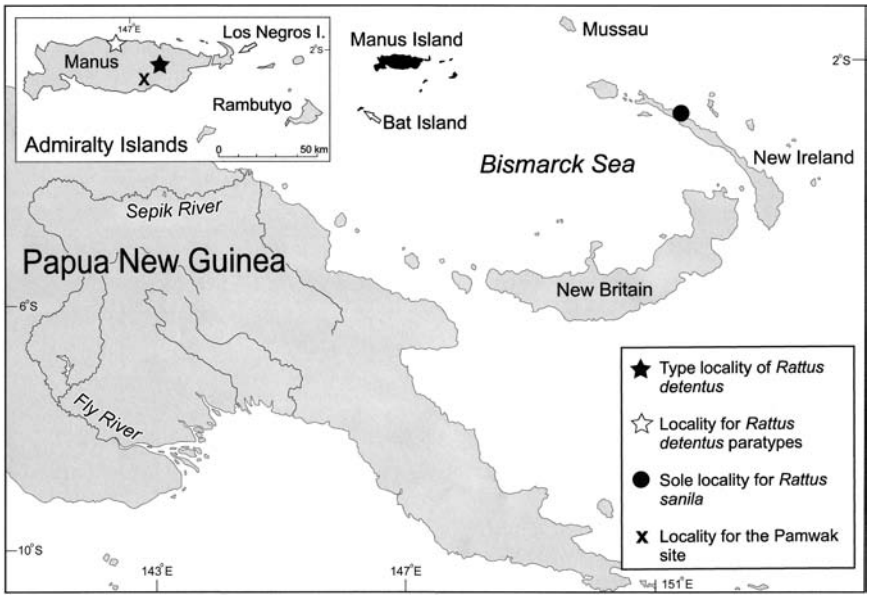

Fig. 3.—Map of the Bismarck Archipelago, Admiralty Islands (in black), and eastern New Guinea, showing the records of *Rattus detentus* on Manus and of the apparently extinct *R. sanila* on New Ireland. All known localities of *R. detentus* are plotted. The closed star represents the type locality, the open star represents the locality of the 2 paratypes, and "X" represents the Pamwak archaeological site. The closed circle represents the Late Pleistocene–Late Holocene Balof 2 archaeological site on New Ireland, the only known locality for *R. sanila*. Manus and Los Negros are separated by a very narrow channel (indicated by a gap).

black guard hairs that are longest posteriorly to a maximum of 55 mm on lower back. Underfur of dorsum and flanks fine and pale gray. Outer surfaces of fore- and hindlimbs paler gray. Ventral fur white to roots and lacks spines—white zone extending from lip to base of tail and 40 mm wide at mid-body, lateral demarcation sharp. Rhinarium white, sides of muzzle with short, dark hairs (Fig. 4). Ears 23.4 mm from notch to rim, clothed in extremely fine hairs, their skin mottled but whiter overall at base, grayer at margin. Mystacial vibrissae stout and black, reaching 60 mm in length (Fig. 4). Skin on dorsal surface of manus and pes speckled with dark pigment, thinly clothed with short, dark hairs. Skin on dorsal surface of all digits white. Palmar surface of manus ivory with irregular gray patches on pads. Pes broad and heavy, 43.2 mm in length (su). Plantar surface dark gray from proximal extremity of heel to proximal edges of plantar pads and then mottled gray and ivory distally onto digits (Fig. 5). Plantar pads broad, flat, and smooth, lacking any trace of striae (Fig. 5). Claws on manus and pes robust, ivory-colored. Tail length 150 mm (57.7% of head + body length), overall color dark gray with paler mottling at very base. Tail scales large, subrectangular, weakly overlapping, dark gray with white skin showing between each row; 6–7 scale rows per cm midway along tail. Three stout bristles emerge from rear of each scale, central bristle longest. Midway along tail, central bristle approximately 1.5 times as long as a scale and outer bristles slightly shorter than scales; near tail tip, central bristles 2–3 times length of scales.

General anatomy of skull and dentition in *R. detentus* (Fig. 6) conforming in all major features with that in other species of *Rattus* (e.g., Greene 1935). Noteworthy features are rostrum elongate and broadened anteriorly; relatively short and bowed incisive foramina that terminate anterior to the molar rows;

Fig. 4.—Anterior portion of *Rattus detentus* (PNGMAG 274363—holotype), showing the coarse dorsal hair; white venter; ear appearing nearly naked; white rhinarium and forefoot; robust, ivory-colored claws; and details of the vibrissae.

interorbital region broad; zygomatic plates broad and tall; palate narrow due to slight outward flexion of molar rows, especially posteriorly; mesopterygoid fossa with narrow, U-shaped anterior margin and broadening to the rear; pterygoid fossa correspondingly narrow; auditory bullae short and uninflated; middle lacerate foramen capacious but separated from postglenoid vacuity by anterior process of ectotympanic; arrangement of stapedial and carotid foramina conforms to inferred primitive murine pattern (described and illustrated by Musser

Fig. 5.—A) Central portion of the tail of *Rattus detentus* (PNGMAG 274363—holotype), showing the large, subrectangular, weakly overlapping scales, with 3 stout bristles emerging from rear of each scale, central bristle longest. B) Right hindfoot of *R. detentus* (PNGMAG 274363—holotype), showing the broad, heavy pes and broad, flat, and smooth plantar pads lacking any trace of striae. Claws on both manus and pes robust and ivory-colored.

1982:5, figure 2D); dentary robust and with prominent capsular process (Fig. 2). Dentition noteworthy for combination of robust incisors with relatively small molars. Upper M1s lacking anterior cingula or accessory cuspules, all upper molars lacking posterior cingulum; cusp t3 weakly developed or absent on M2–3s (Fig. 7). The m1s with 2 cuspids on anteroconid and well-developed posterolabial cusplet; m2s with small anterolabial cuspid and well-developed posterolabial cusplet; m3s with small anterolabial cuspid only (Fig. 7). Upper and lower incisors broad and deep. Ratio of depth to breadth (D/B) of lower incisors 1.67–1.83 (n = 3) and of upper incisors 1.58–1.65 (n = 2).

Measurements of skull and teeth of the 2 most complete modern specimens of *R. detentus* are shown in Table 1. Measurements of the large sample of jaws and teeth of the archaeological specimens from Pamwak are shown in Supporting Information S3. The lower incisor D/B ratio in the archaeological sample ranges 1.44–2.0 (n = 77, $\bar{X}$ = 1.76, SD = 0.122).

The holotype carried 2 fetuses in the uterus, each approximately 1 cm long (crown–rump length).

Morphological comparisons.—Rattus detentus is an exceptionally large and heavy-bodied member of its genus, exceeded in bulk only by mature adult specimens of *R. norvegicus* (Berkenhout, 1769), of *R. everetti* (Günther, 1879) from the Philippine Archipelago, and of *R. jobiensis* from the islands of Cenderawasih (formerly Geelvinck) Bay in northwest New Guinea. Four other species within the Australo–Papuan *Rattus* fauna approach *R. detentus* in size—*R. praetor* of the northern lowlands of New Guinea and the Bismarck Archipelago and Solomon Islands, *R. mordax* of southeast New Guinea and the D'Entrecasteaux Islands and Louisiade Archipelago, *R. leucopus* of the southern lowlands of New Guinea and northeast Australia, and *R. steini* of the central and northern ranges of New Guinea. The recently described *R. nikenii* of Gag Island is comparable to *R. steini* in size. *Rattus sanila* Flannery and White, 1991, a large-toothed species described from Late Pleistocene to Late Holocene contexts on New Ireland and now possibly extinct (see White et al. 1991), also warrants comparison with *R. detentus*. All other Melanesian *Rattus* species are considerably smaller, with adults typically not exceeding 100 g (Taylor et al. 1982; Flannery 1995a). Body proportions also distinguish this suite of smaller Melanesian *Rattus* from *R. detentus*, especially tail length that exceeds 70% of head + body length in all but 1 of the remaining species. The exception is the vole-like *Rattus giluwensis* Hill, 1960, a small (approximately 50–60 g), short-tailed (65% of head + body length) species found in subalpine grasslands of the central ranges of New Guinea (Taylor et al. 1982; Flannery 1995a). Apart from the almost 10-fold disparity in mass, *R. detentus* differs from *R. giluwensis* in numerous cranial features including its proportionally longer rostrum, its short and bowed (versus more elongate and parallel-sided) incisive foramina, and its less inflated auditory bullae (for cranium of *R. giluwensis* see Taylor et al. 1982, figure 28).

Rattus jobiensis has a relatively longer tail (averaging 92.0% of head + body length) and longer, narrower hindfoot (pes length 44.0–51.0 versus 43.2 mm) than *R. detentus*. Its mammary formula is 0 + 1 + 2 = 6 (Yapen and Owi Islands) or 1 + 1 + 2 = 8 (Biak Island). The ventral fur is various hues of yellow to buff but never white. The cranium of *R. jobiensis* (Fig. 6) is elongate and narrow, the nasals are narrower anteriorly than in *R. detentus* (4.8–6.0 versus 6.6–6.9 mm), the auditory bulla is more inflated, the interorbital region is narrower (6.2–7.3 versus 8.1–8.2 mm), the mesopterygoid fossa is narrower and parallel-sided (Fig. 6), and cusp t3 is larger on M2–3s (Fig. 7).

Rattus leucopus is a smaller rat (maximum mass 315 g—Flannery 1995a) with a narrower hindfoot and longer tail (tail length averaging 84.7–89.9% of head + body length in the 3 New Guinean subspecies). The mammary formula is 0 + 1 + 2 in all subspecies. The cranium has a more slender rostrum (Fig. 6) with narrower nasals (anterior width 3.9–6.3 mm across all subspecies), a narrower interorbital region (5.5–8.2 mm), less robust zygomatic plate, and a parallel-sided mesopterygoid fossa (for cranium of *R. leucopus* see Taylor et al. 1982, figure 19 and Flannery 1995a, Plate 36).

Rattus mordax is a smaller rat (maximum recorded mass 255 g—Flannery 1995b) with tail length averaging 83.5% of head +

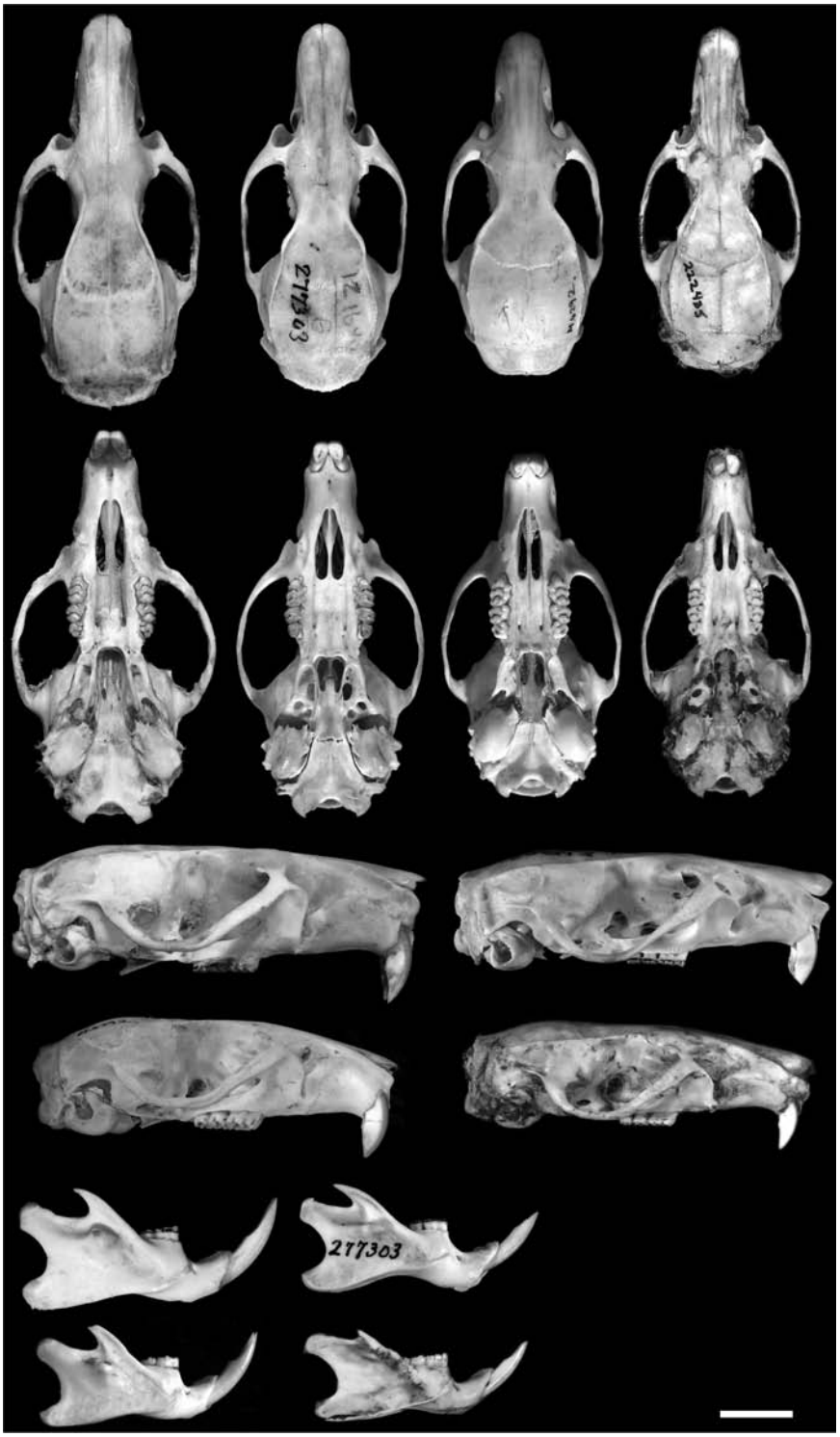

Fig. 6.—Crania and dentaries of 4 species of *Rattus* from Melanesia. Crania (dorsal and ventral) from left to right = *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), and *R. jobiensis* (AMNH 222435). Lateral views of crania: upper row, left to right, *R. detentus* and *R. praetor*; lower row, left to right, *R. mordax* and *R. jobiensis*. Dentaries: upper row, left to right, *R. detentus* and *R. praetor*; lower row, left to right, *R. mordax* and *R. jobiensis*.

body length in *R. m. mordax* and 82.1% in *R. m. fergussoniensis* (Taylor et al. 1982). Its dorsal fur is less spiny than that of *R. detentus* and is "yellowish ivory with the medium gray underfur showing beneath" (Taylor et al. 1982:228). The cranium of *R. mordax* (Fig. 6) has straight-sided incisive foramina; a short and narrower rostrum with anterior nasal width of 3.8–6.0 mm (across both subspecies); a wide, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin; larger and more inflated auditory bulla; a narrower interorbital region (5.2–7.1 mm); strongly flared temporal ridges; and M2–3s with a larger cusp t3 (Fig. 7).

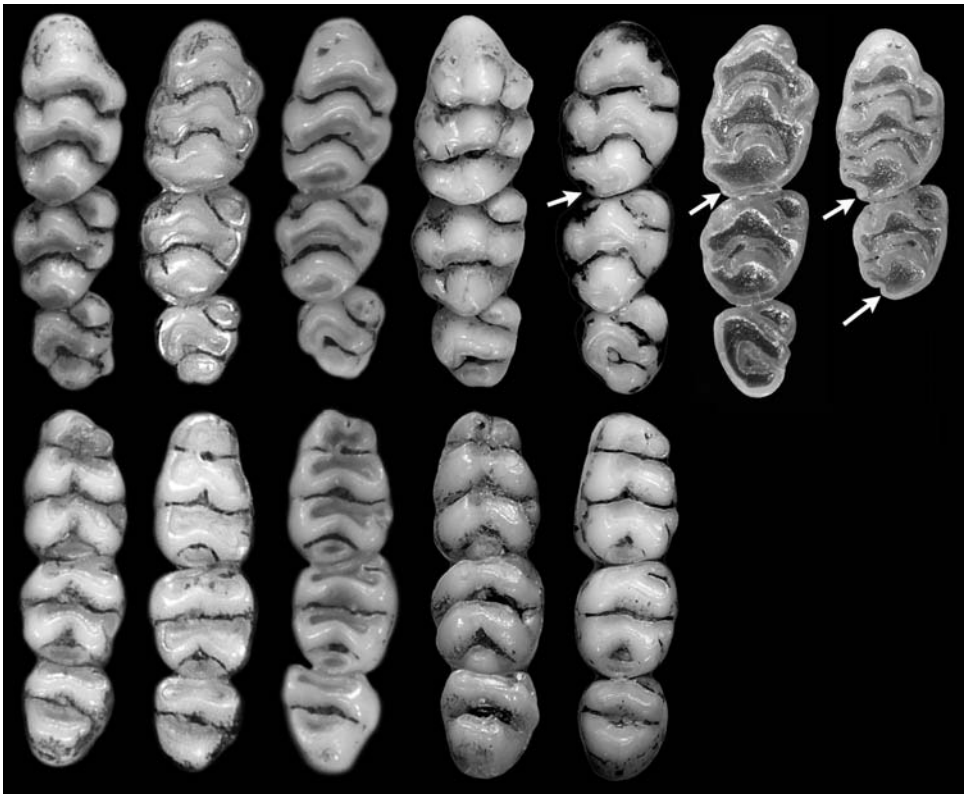

Fig. 7.—Top: upper right molar toothrows, from left to right, of *Rattus detentus* (KU 163723—a paratype), *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), *R. jobiensis* (AMNH 222435); upper left toothrows (image reversed), from left to right, of *R. sanila* (AMS F82021—holotype), *R. sanila* (AMS F89058). Arrows point to posterior cingula present only on upper molars of *R. jobiensis* and *R. sanila*. Bottom, left to right: lower right toothrows of *R. detentus* (KU 163723—a paratype), *R. detentus* (PNGMAG 274363—holotype), *R. praetor* (USNM 277303), *R. mordax* (AMS M4292), *R. jobiensis* (AMNH 222435). Anterior is at the top. Images not to scale but made to be of similar size for ease of comparison.

Rattus praetor is a smaller rat (maximum recorded mass 240 g—Flannery 1995a, 1995b) with a longer tail (averaging 78.1% of head + body length in *R. p. praetor* and 89.4% in *R. p. coenorum* (Taylor et al. 1982). Its dorsal fur is less spiny than that of *R. detentus* and it has yellowish or gray rather than white ventral fur. The cranium of *R. praetor* (Fig. 6) typically has incisive foramina that are more broadly rounded at the rear; a wider, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin; larger and more inflated auditory bulla; a narrower interorbital region (5.4–7.3 mm across both subspecies); M1s with less distinct labial cusps t3 and t6; and M2s with a larger cusp t3 (Fig. 7). *R. praetor* resembles *R. detentus* in the degree of anterior widening of the rostrum (Fig. 6).

Rattus steini is a smaller rat (maximum recorded mass 220 g—Flannery 1995a) with shorter hindfoot (maximum recorded pes length of 38 mm—Taylor et al. 1982) and a longer tail (averaging 86.0–101.5% of head + body length in the 4 recognized subspecies—Taylor et al. 1982). Its dorsal fur is less spiny than that of *R. detentus* and it has yellowish or gray rather than white ventral fur. Its mammary formula is 0 + 1 + 2 = 6 (*R. s. steini* and *R. s. baliemensis* Taylor, Calaby, and Van Deusen, 1982) or 1 + 1 + 2 = 8 (*R. s. foersteri* Rümmler, 1935 and *R. s. hageni* Troughton, 1937). The cranium of *R. steini* (see Taylor et al. 1982, figure 23 and Flannery 1995a, Plate 34) has less robust zygomatic plate, a wider, parallel-sided mesopterygoid fossa with a square rather than rounded anterior margin, and a narrower interorbital region (4.9–7.2 mm across all subspecies).

The rats of Gag Island, described as *R. nikenii*, are even smaller (maximum recorded mass 175 g, maximum recorded pes length 36.5 mm), and have a tail that approaches head + body length (Maryanto et al. 2010). Based on our examination of the published images, the cranium closely resembles that of *R. steini*.

Rattus sanila has larger molars (length of M1 = 4.3–4.8 mm; n = 3; width of M1 = 2.6–2.7 mm; n = 3) than *R. detentus* and a more complex molar morphology that features an anterior cingular ridge on M1s, prominent posterior cingula on M1–2s, larger cusp t3 on M2–3s and more prominent posterior longitudinal ridges on cusps t1 and t4 of M1s and cusp t4 of M2s (Fig. 7). The upper and lower incisors of *R. sanila* are less robust than those of *R. detentus*. No further comparisons with *R. sanila* are possible because it is known only from dentaries, partial maxillae, and isolated teeth.

Bivariate plots of posterior rostral width against condylobasal length (Fig. 8A) show that the condition in *R. detentus* is consistent with observed intra- and interspecific allometry among other New Guinean *Rattus*. However, an equivalent plot for anterior rostral width (Fig. 8B) shows that *R. praetor* and

Table 1.—External, cranial, and tooth measurements (in mm) of 2 of the modern specimens of *Rattus detentus* (holotype PNGMAG 274363 and paratype KU 163723) and selected related species (means in mm).

Measurements	PNGMAG 274363	KU 163723[a]	*R. jobiensis*	*R. leucopus*	*R. mordax*	*R. praetor*
Head and body length	260	—	—	—	—	—
Tail length	150	—	190 (n = 2)	157.7 (n = 111)	152.2 (n = 60)	144.4 (n = 113)
Length of hind foot (s.u.)	43.2	—	45.8 (n = 2)	37.0 (n = 128)	36.2 (n = 53)	35.2 (n = 114)
Length of ear	23.4	—	22.8 (n = 2)	21 (n = 1)	19.5 (n = 17)	19.5 (n = 60)
Condylobasal length	52.0	48.72	—	—	—	—
Zygomatic breadth	27.35	24.57	—	—	—	—
Lambdoidal breadth	19.55	19.93	—	—	—	—
Occipitonasal length	53.45	49.99	—	—	—	—
Length of rostrum	7.3	8.46	—	—	—	—
Breadth of rostrum	10.85	9.72	—	—	—	—
Width of zygomatic plate	4.9	5.58	—	—	—	—
Interorbital width	8.2	8.08	—	—	—	—
Nasal length	20.55	18.99	—	—	—	—
Width across nasals	6.6	6.9	—	—	—	—
Length of bony palate	10.55	10.71	—	—	—	—
Length of upper diastema	15.5	12.84	—	—	—	—
Length of incisive foramen	9.65	8.22	—	—	—	—
Width across incisive foramina	3.85	3.25	—	—	—	—
Postpalatal length	7.45	8.81	—	—	—	—
Mesopterygoid fossa width	3.55	2.88	—	—	—	—
Length of auditory bulla	7.35	6.94	—	—	—	—
Crown length of upper toothrow	8.4	8.71	—	—	—	—
M1–3 alveolar length	8.6	9.44	—	—	—	—
Width across M1–M1 (outside)	5.66	9.2	—	—	—	—
Upper incisor width	2.0	1.7	—	—	—	—
Upper incisor depth	3.3	2.68	—	—	—	—
Width of M1	2.55	2.57	—	—	—	—
Width of M2	1.78	1.94	—	—	—	—
Width of M3	1.95	1.95	—	—	—	—
m1–3 crown length	8.3	8.67	—	—	—	—
Width of m1	2.15	2.21	—	—	—	—
Width of m2	2.4	2.48	—	—	—	—
Width of m3	2.25	2.2	—	—	—	—
Lower incisor width	1.75	1.38	—	—	—	—
Lower incisor depth	3.1	2.3	—	—	—	

[a] Because KU 163723 had the remaining soft tissues removed from it by its being buried in the ground for a period, the elements of the skull posterior to the frontals and the palatines became dissociated before and during the final cleaning. Some measurements for KU 163723 may deviate slightly from the original because some separated bones have been glued back in place but we are confident that such deviation is extremely minimal, as adjacent cranial bones fit together properly.

R. detentus alone have an unusual degree of anterior rostral inflation. The unusual deepening of the lower incisors in *R. detentus*, compared with the conditions in other large Melanesian *Rattus*, including *R. sanila*, is also evident from a bivariate plot (Fig. 8C). The upper incisors are similarly distinguished by their proportional depth in *R. detentus*.

Molecular genetics.—Concatenation of the 3 nuclear loci and the mitochondrial *CR* resulted in an alignment of 4,166 bp in length for 73 specimens comprising 24 species/subspecies. The topology of both the Bayesian and maximum likelihood trees concurred in showing the following well-supported species groups (Fig. 9): Clade E: *R. niobe* (Thomas, 1906) + *R. mordax*; Clade F: other New Guinean *Rattus*; Clade G: *R. leucopus*; Clade H: *R. fuscipes* (Waterhouse, 1839); and Clade I: other Australian *Rattus*. *R. detentus* is placed outside of each of these well-supported clades and thus appears to be a phylogenetically isolated lineage in its own right. However, its placement on the tree as the immediate sister to all endemic New Guinean *Rattus* does not have robust support (Fig. 9). The genetic evidence thus provides strong independent support for our conclusion that the Admiralties Rat represents a very distinct species within the Australo–Papuan *Rattus* radiation.

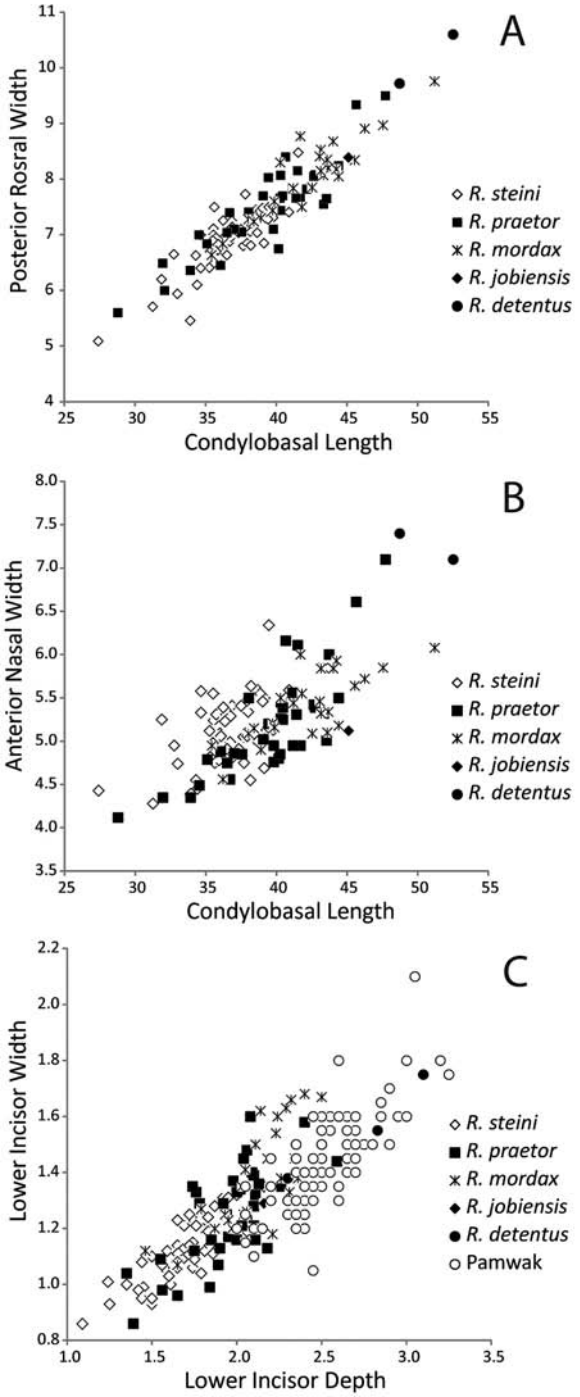

Fig. 8.—Bivariate plots of selected cranial and dental dimensions in *Rattus detentus* and a range of other Melanesian *Rattus* species. A) Plot of posterior rostral width against condylobasal length. B) Plot of anterior rostral width against condylobasal length. C) Plot of lower incisor width against lower incisor depth.

The majority (72%) of parsimony informative (pi) sites (300 pi sites) were derived from the mitochondrial *CR*, compared to 28% in total among the 3 nuclear genes (*FGB*: 31 pi sites; *DHFR*: 48 pi sites; *ATP5A1*: 36 pi sites). Trees generated from the mitochondrial *CR* data only (Supporting Information S4) and from a concatenation of the 3 nuclear genes only (Supporting Information S5) differ from the tree generated from the combined data in the following ways: nodes B and C are absent from the mitochondrial *CR* tree, whereas in the nuclear gene tree nodes B, C, E, H, I, J, and K are all absent. As might be expected from the large difference in pi sites, the mitochondrial *CR* data clearly supply much of the topology of the combined dataset tree. Nevertheless, *R. detentus* is identified as a highly divergent lineage from all other Australo–Papuan *Rattus* groups in each of the separate mitochondrial *CR* and concatenated nuclear trees.

Additional mitochondrial *CR* sequences for Australo–Papuan *Rattus* are available from the studies of Rowe et al. (2011) and Robins et al. (2014). Inclusion of these sequences produces an alignment of 104 Australo–Papuan *Rattus* individuals representing 23 putative species and subspecies. As noted previously by Robins et al. (2014), phylogenetic analysis of this dataset (Supporting Information S6) identifies a number of potential cryptic species among each of the 2 montane New Guinean "species" *R. niobe* and *R. verecundus* (Thomas, 1904b). However, none of the additional *CR* lineages shows special affinity to *R. detentus*, which maintains its isolated position within the Australo–Papuan *Rattus* radiation.

Ecology and other notes.—In 2012, the vegetation around Kawaliap Village, in the immediate vicinity of the collection locality, was a mosaic of *Metroxylon* (sago) palms (Arecaceae), mixed tapioca (*Manihot esculenta*, Euphorbiaceae) and vegetable gardens, and secondary regrowth scrub (Fig. 1E).

The holotype was caught in a snare set by local hunters targeting bandicoots (*Echymipera* cf. *kalubu*) and rats. Both are consumed. Unbaited snares were set along visible paths made by small mammals through undergrowth and often exiting near small streams. Other evidence of rat activity in this habitat included conspicuous incisor gnawing marks on fallen nuts of *Canarium indicum* (Burseraceae)—a semidomesticated Melanesian tree species that is widely cultivated and commonly consumed by rodents (Fig. 1B).

The local language name provided to Weijola at Kawaliap Village for this rat was *Wadah* (pronunciation "Warah"). Ann Williams (in litt.) informed us that inhabitants of Tulu No. 1 identified the remains of the 2 paratypes as examples of *Musuru*; the same name is listed by Flannery (1995b; as *Musirou*) as an indigenous name for *M. matambuai*. Williams also recorded the local names *Sopol* and *Pitiy* as possibly referring to rats. Manus Island supports more than 15 indigenous languages (Lynch et al. 2002) and some diversity in local names is to be expected.

In October 2014, Aplin spent 2 weeks on Manus Island as a participant in a Wildlife Conservation Society (WCS) survey (Aplin et al. 2015). Two sites were surveyed—the upper slopes of Mt. Sabomu (2°11′36″S, 146°50′00″E; the 2nd highest peak on Manus Island) at elevations ranging from 300 to 570 m, and Yeri River (2°0′06″S, 146°48′50″E) at elevations of 22–84 m. These sites were selected because they presented a mosaic of disturbed to relatively intact forest habitats but at contrasting elevations. The Yeri River locality is close to the paratype locality of Tulu No. 1 and presented comparable habitat. Both sites were sampled using a combination of trapping, camera trapping, spotlighting, and active searching for tracks and signs. Survey effort at Mt. Sabomu was 178 snap-trap nights and 44

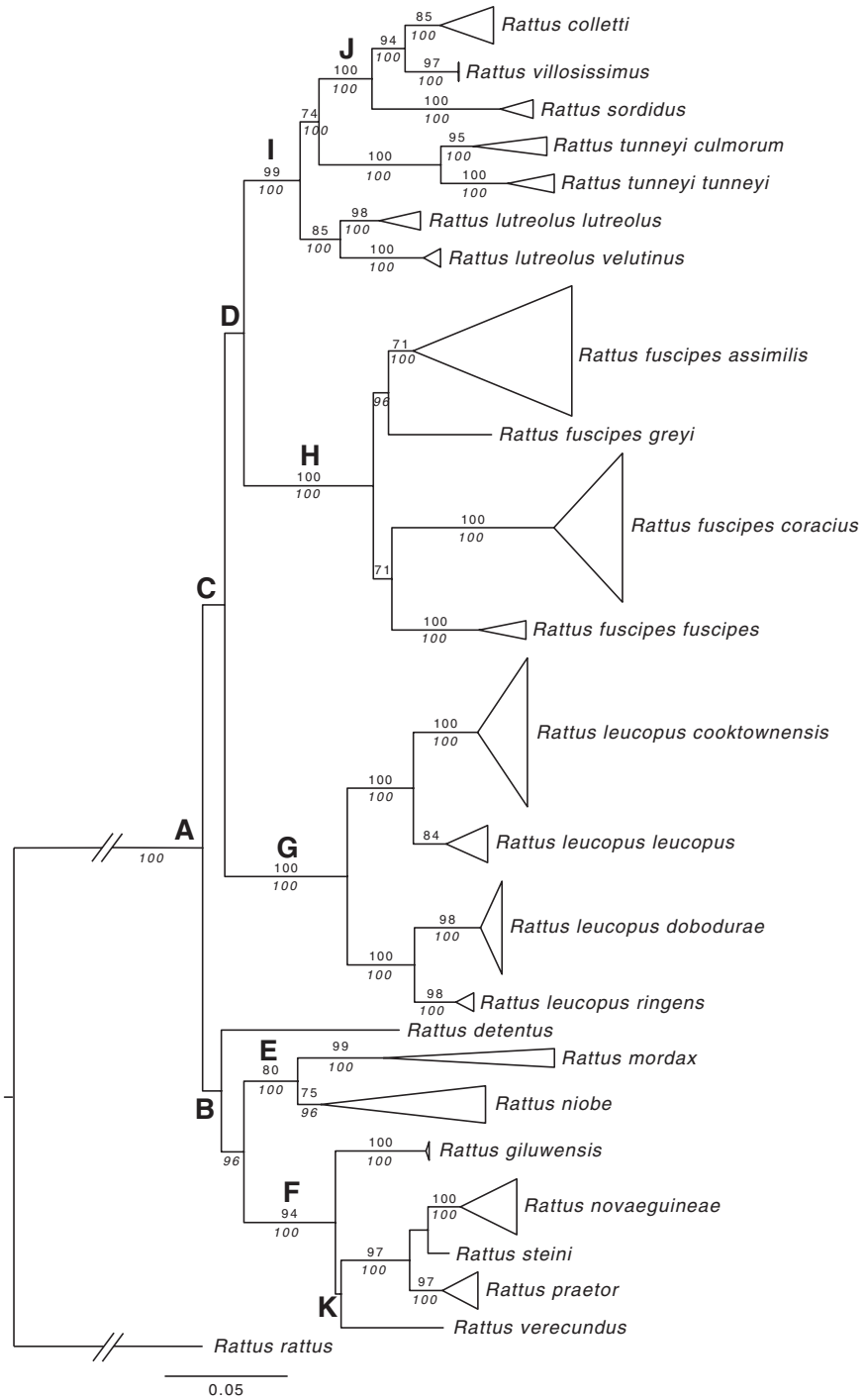

Fig. 9.—Collapsed maximum likelihood tree from a concatenated analysis of Australo–Papuan *Rattus* and selected outgroups, based on the mitochondrial *control region* and 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB*. Nodal support is indicated by maximum likelihood bootstrap proportions above branches and Bayesian posterior probabilities values below branches. Nodes discussed in the text are labeled A–K.

camera-trap nights; and at Yeri River, 204 snaps-trap nights and 64 camera-trap nights.

Trapping produced a few individuals of *R. exulans* at each of Mt. Sabomu [1 in forest and 2 in kunai (*Imperata cylindrical*; Poaceae) grassland] and Yeri River (2 in forest and 6 in gardens) but no individuals of *R. detentus*. Camera trapping also produced images of *R. exulans* at both sites, including 1 individual in forest on Mt. Sabomu that appeared to be occupying a burrow complex with multiple entrances, spread over an area of ca. 10 m^2. Elsewhere in New Guinea, *R. exulans* typically constructs leaf or grass nests above ground but it has on occasion been found in burrows (Aplin et al. 2003), most likely excavated by other species. *Echymipera* cf. *kalubu* bandicoots do not excavate burrows but construct leaf nests in crevices or shallow depressions (Andersen et al. 1988). We suspect that the burrow complex on Mt. Sabomu

was excavated by *R. detentus* but confirmation in the form of a capture or image is required. At both sites, intensive but unsuccessful searches for other traces of a relatively large rat, such as footprints, diggings, or chewed nuts or woody endocarps, were made along stream margins, under overhanging rocks, and at the bases of buttressed trees. Elsewhere in Melanesia, large *Rattus* species are usually among the easiest of terrestrial mammals to trap and otherwise detect from footprints in areas of damp soil, and from feeding debris and feces in sheltered areas among rocks and inside logs. The lack of such signs at both survey sites suggests that *R. detentus* was either absent or present only in very low numbers during the survey period.

Discussion

The rodent fauna of the Admiralty Group.—With formal description of *R. detentus*, the inventory of the extant native rodents for Manus Island is most likely complete. While it is true that many parts of the island remain unsurveyed, the absence of additional taxa in the large sample of rodents from the Pamwak archaeological site makes it unlikely that any additional rodent species will be found alive on Manus Island. Even so, it is worth noting that the Pamwak mammal record spans only the last 9,000 years of a human occupation history that probably extends back 40,000 years or more, given the regional evidence of remote seafaring by early Melanesian human populations (Leavesley and Chappell 2004). In light of this still undocumented early history of human–animal interactions in the Admiralty Group, we leave open the possibility that the original rodent fauna of Manus may have included a wider range of endemic taxa, including some that fell victim to the usual threats associated with human arrival on oceanic islands.

The mammal faunas of the other islands of the Admiralty Group remain largely unstudied, and most islands are probably too small to support any native rodents. However, further survey effort is needed to determine whether any of these smaller islands support populations of either of the 2 Admiralty Island endemic rodents or any other species of rodents. The St. Matthias Group also remains poorly surveyed for mammals. However, a recent visit by Aplin as part of a WCS team failed to locate any native rodent species on Mussau Island, the largest island of the group (Aplin et al. 2015).

Phyletic patterning in Melanesian Rattus.—Rattus detentus appears to represent a deeply divergent phyletic lineage among Australo–Papuan *Rattus*. Rowe et al. (2011) estimated the initial divergence of this clade at 1.05 Ma (*CI* 0.85–1.28 Ma). Although we did not subject the expanded taxon set to a new divergence date estimation, the fact that inclusion of *R. detentus* in the phylogeny did not cause any other shifts in topology suggests that this molecular divergence estimate will remain largely intact. Accordingly, we regard the lineage leading to *R. detentus* to have diverged from all other sampled lineages around the transition from the Early to Middle Pleistocene. Whether or not this also represents the time of dispersal of *Rattus* to Manus Island is less certain, as consideration might be given to the alternative scenario that divergence of this lineage was underway prior to its dispersal to the island. The latter scenario might be particularly viable if the ancestor of *R. detentus* came from the main island of New Guinea, rather than entering the Admiralties as part of an initial wave of dispersal of *Rattus* into the Melanesian region from the west. These alternatives are testable through the discovery of fossil rodents of sufficient antiquity either in the Admiralties or on the main island of New Guinea.

Vertebrate biogeography of the Admiralty Group.—Estimates of 8–10 million years before present (ybp) for initial subaerial emergence of Manus (Allison 1996) should probably be revised down to the early Pliocene (approximately 4–5 million ybp) in light of new dating of regional tectonic events (see Davies 2012 and references therein). Irrespective of the initial emergence time, deep water basins surrounded the Admiralties throughout the Pliocene to Recent, hence they remained isolated from other land masses through the sea-level fluctuations associated with Quaternary glacial cycles (Voris 2000). Thus, by whatever means, the fauna of the Admiralties must have arrived through overwater dispersal.

The Admiralties are one of a series of island groups that are located north and northeast of New Guinea and which are collectively known as the Northern Melanesian Islands. With the exception of the land-bridge island of Yapen, all of these islands are oceanic in origin.

Despite widely scattered positions, the northern Melanesian islands share striking similarities in their terrestrial vertebrate faunas. Endemic marsupial taxa include 2 species of *Spilocuscus—S. wilsoni* on Biak/Supiori and *S. kraemeri* in the Admiralties, and possibly 1 *Petaurus* (*P. biacensis*, see Flannery 1995b) on Biak/Supiori. Endemic subspecies (*Phalanger orientalis breviceps* and *Echymipera kalubu philipi*) have been described from New Britain and Biak/Supiori, respectively, but their taxonomic status requires confirmation.

Each island group also hosts endemic murids. The Admiralties have 2 species—*M. matambuai* and *R. detentus*. Biak Island in the Schouten Group has 2 endemic giant rats (*Uromys boeadii* Groves and Flannery, 1994, and *U. emmae* Groves and Flannery, 1994), a large *Rattus* (*R. jobiensis*), and taxonomically undifferentiated populations of a mosaic-tailed rat [*Paramelomys platyops* (Thomas, 1906)] and the widespread Australo–Papuan Water Rat (*Hydromys chrysogaster* É. Geoffroy St.-Hilaire, 1804). The same species of *Hydromys*, *Paramelomys*, and *Rattus* are present on Supiori. New Britain has an endemic water rat (*H. neobrittanicus* Tate and Archbold, 1935), the highly distinctive *U. neobrittanicus*, the widely distributed *M. rufescens* (Alston, 1877) and an undescribed endemic *Melomys* (Aplin and Opiang 2011), a potentially endemic *Pogonomys* tree mouse, and 2 other, undescribed, endemic species, each of an endemic genus (Aplin and Opiang 2011). New Britain also supports a *Rattus* species at least superficially similar to *R. praetor* but warranting genetic examination (Flannery 1995b; Aplin and Opiang 2011). By contrast, the murid fauna of New Ireland is depauperate, with only 2 taxa—the seemingly widespread *M. rufescens* and the endemic and apparently extinct *R. sanila*.

Manus and New Ireland stand out in lacking larger murines of the genera *Hydromys* and *Uromys*. The only clearly indigenous terrestrial mammals on these islands are the closely related species pair *M. matambuai* and *M. rufescens* (Flannery et al. 1994) and a large endemic *Rattus*. This paucity is surprising considering their size and may reflect their relative isolation (Manus) or the timing of subaerial emergence [New Ireland became emergent during the Pleistocene (see Davies 2012 and references therein)].

Levels of endemism in other groups of animals on these islands are also instructive. The herpetofauna of the Admiralties is still incompletely described, but recent surveys have documented 8 endemic species of ceratobatrachid frogs of the genus *Cornufer*, along with 2 widespread hylid frogs and 1 widespread ranid frog (Richards and Aplin 2015)—the invasive bufonid *Rhinella marina* also occurs there. The agamid *Hypsilurus schoedei*, described from Rambutyo Island in the Admiralties, is now also recorded from Mussau Island in the St. Matthias Group (Richards and Aplin 2015). The monitor lizard of the Admiralties, *Varanus cf. indicus*, differs notably from populations of northern New Guinea, with molecular studies placing it as one of the most "basal" lineages among mangrove monitors (V. Weijola, pers. obs.). Scincids and gekkonids of the Admiralties are more diverse, with 22 recorded species across the 2 families. However, only 1 gecko and 4 skinks are endemic to the Admiralties; the majority are so-called "tramp species" that seem adept at long water crossings either through natural means or accidental human transport. The situation vis-à-vis endemic status for the very few species of snakes is uncertain. The large air-breathing land snail *Papustyla pulcherrima* (Camaenidae) is a significant invertebrate endemic.

Significant endemism is seen in bats (Aplin et al. 2015; Armstrong et al. 2015) and birds (Mayr and Diamond 2001; Dutson 2011) in the northern Melanesian islands. Many species of bats are shared between Manus and the St. Matthias Group but 1 or more species are likely to be endemic to the Admiralties (Aplin et al. 2015).

Some of the nonflying species may have made the 1st part of their journey to the Admiralties via the Sepik River, which currently debouches on the north coast of New Guinea some 300 km to the southwest of Manus. However, in the Middle Pleistocene, the Sepik Basin was a shallow marine environment (Chappell 2005), and the river mouth must have been more distant from Manus. Nevertheless, it may have still been influential. While at sea between New Guinea and the Admiralties in the late 1980s, Flannery observed rafts of vegetation, some with trees still in growth position, far from land. Some rafts were large enough to provide temporary habitat for small rodents, lizards, frogs, and terrestrial snails. At various times through the Pliocene and Pleistocene, similar rafts may have been carried as far north as the Admiralties. For a more detailed account, see Flannery (2011).

The extent to which deliberate human introductions have shaped the insular distributions remains imperfectly known. New Ireland has the longest archaeological record in the region and many of the key sites contain vertebrate faunal remains (Flannery and White 1991; Leavesley and Chappell 2004). In addition to pigs, dogs, and 2 semicommensal rats (*R. exulans* and *R. praetor*), all of which were introduced within the past 4,000 years, marsupials were also carried to New Ireland. The phalangerid *Phalanger orientalis breviceps* was introduced to the island in the early Holocene, and the macropodid *Thylogale browni* in the mid-Holocene (Flannery and White 1991). New Britain still lacks an equivalent archaeological faunal record and the status of its nonendemic marsupials and rodents is unresolved (Aplin and Opiang 2011). The same uncertainly applies also to Manus—the Pamwak site documents the presence of the bandicoot and cuscus by the early Holocene but it does not rule out their introduction at an earlier date. In spite of these uncertainties, the discovery of *R. detentus*, along with the summary of endemic insular forms, provided here, demonstrates that nonanthropogenic overwater dispersal in the northern Melanesian islands has been less difficult and more extensive than might be and has been imagined.

Conservation.—Rattus detentus is recorded with certainty from only 2 modern localities and 1 prehistoric rock shelter site on Manus. Although these records span a narrow elevational range from near sea level to 200 m, other components of the forest biota of Manus show little evidence of elevational zonation (see various chapters in Whitmore 2015). Thus, it is likely that *R. detentus* occupies or has occupied the full elevational range on Manus, as suggested also by the tentative attribution to this species of a burrow complex near the summit of Mt. Sabomu, reported herein. How much of its potential range on Manus is occupied and whether it occurs on some of the other Admiralty Islands, especially Los Negros, is unknown.

By the mid-1990s, 80% of forest on Manus was still largely intact, whereas many of the smaller adjacent islands had been converted into coconut plantations (Rannells 1995). Today, most of the lowlands on Manus are a mosaic of plantations and/or subsistence gardens and secondary forest, and logging is carried out in many areas. Intact lowland forest is confined to small patches such as those along the Yeri River, visited by Aplin in 2014. Away from the coast, steeper terrain generally supports more or less intact forest which is visited by people in search of game (chiefly the cuscus and wild pigs) and other forest products.

Local residents who were shown photographs of the holotype of *R. detentus* by Weijola claimed that the species is widespread on Manus and also occurs on adjacent Los Negros. The species does appear to possess some tolerance of habitat disturbance and human predation, as the 2 modern capture records both came from regrowth forest and gardens, and derive from the efforts of hunters. However, Aplin's recent failure to locate the species at 2 sites on Manus, with both sites sampled across a gradient of disturbance, suggests that *R. detentus* is not universally common. If it is present at the Mt. Sabomu and Yeri River sites, then it appears to survive only at low population densities. Thus, it would likely be erroneous to treat the species as secure across its range, and we urge further survey work to locate surviving populations, so as to enable study of their population dynamics, and to identify major threats to their continued existence.

Three of the most likely threats to the survival of *R. detentus* are habitat conversion and disturbance, feral cats (*Felis catus*), and the spread of introduced rodents.

Cats were introduced to Manus sometime in the 19th or 20th centuries and the occurrence of feral populations is reported from several areas by local residents. However, the WCS survey in 2014 failed to detect any sign of feral cats at its 2 survey sites (Aplin et al. 2015) and this suggests that either feral cats are not ubiquitous or that population densities are sometimes very low.

Two introduced rodents, *R. exulans* and *R. rattus*, are present on Manus (Taylor et al. 1982; Aplin et al. 2015). *R. exulans* may have arrived in prehistoric times, although there is no apparent evidence for this from the Pamwak site. *R. rattus* most likely arrived in colonial times or later. *R. exulans* is clearly widespread and occurs across a variety of habitats, including the remote and relatively undisturbed forest near the summit of Mt. Sabomu (Aplin et al. 2015). However, while it may be common in certain habitats, including villages, gardens, and patches of kunai grassland, it appears not to be universally abundant in forest. Given the rarity of introduced rats in the forests, interspecific competition seems unlikely as a sufficient explanation for the apparent rarity of *R. detentus* there.

Elsewhere, the introduction of *R. rattus* has been implicated in the extinction of insular native rats. *R. macleari* (Thomas, 1887) and *R. nativitatis* (Thomas, 1889), 2 endemics of Christmas Island, became extinct around 1903 (Flannery 1990)—the proximate cause may have been a trypanosome carried by *R. rattus* which reached the island at around this time (Wyatt et al. 2008). On Manus, *R. rattus* does not yet appear to be widely invasive into rural regions and/or natural habitats. Whether the Manus population carries a pathogenic trypanosome is unknown.

A regional example of insular decline or possible extinction involves *R. sanila*, thus far known only from Pleistocene to Late Holocene rock shelter deposits on New Ireland. White et al. (1991, 2000) postulated that this species was replaced ecologically by *R. praetor*, a New Guinean species that reached the island within the last few millennia, probably with human assistance. Whether or not this view is correct, there are grounds for concern that inadvertent introduction to Manus Island of *R. praetor*, if this has not already occurred, might contribute to the decline of *R. detentus*.

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Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the authors that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the authors.

Supporting Information S1.—List of specimens analyzed for the morphological comparisons. Specimens are arranged by species, then locality information (generally as given in information currently associated with specimens). Archaeological material listed by site. Museum catalog numbers follow the institutional acronyms given in "Materials and Methods."

Supporting Information S2.—Taxon, catalog number, collection depository, locality where collected, and GenBank accession numbers for sequences used in phylogenetic analyses.

Supporting Information S3.—Measurements of the lower and upper dentitions, mandibular ramus, and maxilla of specimens of *Rattus detentus* from the Pamwak archaeological site.

Supporting Information S4.—Collapsed Bayesian tree of Australo–Papuan *Rattus*, based on the mitochondrial *control region* and using *Rattus rattus* as the outgroup. Nodal support is indicated by maximum likelihood bootstrap above branches and Bayesian posterior probabilities values below branches. Nodes are labeled A–K as per Fig. 9. Data associated with specimens of *R. fuscipes assimilis* are from Rowe et al. (2011) and Robins et al. (2014), from whence the numbers associated with the specimens were obtained.

Supporting Information S5.—Collapsed Bayesian tree of Australo–Papuan *Rattus*, based on concatenated sequences of 3 nuclear genes—*ATP5A1*, *DHFR*, and *FGB*—and using *R. rattus*

as the outgroup. Nodal support is indicated by maximum likelihood (ML) bootstrap above branches and Bayesian posterior probabilities values below branches. Nodes are labeled A–K as per Fig. 9. The stars represent branches not present in the ML tree (i.e., these branches collapse to a polytomy). Data are from Rowe et al. (2011) and Robins et al. (2014), from whence the numbers associated with the specimens were obtained.

Supporting Information S6.—Maximum likelihood tree of relationships among mitochondrial *CR* sequences from a more extensive sampling of Australo–Papuan *Rattus*, drawn from combining data from this study with that of Rowe et al. (2011) and Robins et al. (2014). Numbers associated with the specimens include GenBank number and institution acronym. *Sundamys muelleri* (Jentink, 1879) and selected species of *Rattus* are used as outgroups.

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SI 1
Specimens Examined

List of specimens analyzed for morphological comparisons. Specimens are arranged by species, then locality information (generally as given in information currently associated with specimens). Archaeological material listed by site. Museum catalog numbers follow the institutional acronyms given in Materials and Methods.

Rattus argentiventer (Robinson and Kloss, 1916) (3).—Indonesia: Bentiang NW Borneo (109°54′E) [1♂, 1♀, AMS 11917–18]. Portugese Timor; 12 km SW Suai [1 sex ?, AMS 15287]; Betano [1♀, AMS 17813].

Rattus detentus (3 Recent + 191 archaeological).—Papua New Guinea: Manus Province; Admiralty Islands, Manus Island, Kawaliap Village, el. 200 m (2°6′40″S, 147°3′40″E) [1♀, AMS 45608—holotype]; Tulu no. 1, el. 34 m (01°57′37″S, 146°50′28″E) [sex ?, KU 163723–24—paratypes]; Pamwak Archaeological Site, SSE of Piterait, 4 km inland from coast, el. 30 m (Fredericksen et al. 1993), 191 unnumbered specimens, some dentaries retaining 3, 2, or 1 molars, but primarily isolated incisors and molars.

Rattus elaphinus Sody, 1941 (6).—Indonesia: North Moluccas; Sula Island Group, Manggole Island, Cepalulu Village (1°53′S, 125°50′E) [3♂♂, 1♀, 1 sex ?, AMS 26436, 26609–11, 26964, 26966].

Rattus exulans (51).—Papua New Guinea: Aitape, Sepik Div. (3°09′S, 142°21′E) [1♂, 2♀, 1 sex ?, AMS 3721–22, 6215, 6233]; Bismarck Archipelago, Duke of York Island (4°10′S, 152°28′E) [2♂♂, AMS 2364–65]; Bulolo Morobe Division (7°12′S, 146°39′E) [2♂♂, 3♀♀, AMS 6382–

86]; British New Guinea, Fife Bay (10°35′S, 150°00′E) [1♂, 1 sex ?, AMS 2483–84]; Buin District, Bougainville, 10 mi inland (6°50′S, 155°45′E) [2♂♂, 1♀, AMS 6494–96, 2♀♀, AMS 6648–49]; Dobodura North Division (8 46' S, 148 23' E) [7♂♂, 4♀♀, 6918–22, 6962–6966, 6978–6979]; Kiriwina Trobriand group NZ (8°28′S, 151°05′E) [1♂, AMS 1146]; Mt. Hagen District, Sepik Div. (5°54′S, 144°09′E) [2♂♂, 1♀, AMS 6110–6112]; Marshall Bennett Group, Gawa Is. (8°59′S, 151°58′E) [1♀, AMS 6370]; Mt. Lamington District, Northern Div. (8°50′S, 148°08′E) [4♂♂, 4♀♀, 1 sex ?, AMS 4152–4158, 4298–4299, 4688]; New Britain; Aviklo Village Mowehaffen (6°12′S, 149°30′E) [1♂, AMS 5621]; Marshall Bennett Group, Gawa Is. (8°59′S, 151°58′E) [1♀, AMS 6370]; Admiralty Group, Purdy Islands, Bat Is. (2°51′S, 146°14′E) [1♀, ASM 6976]; Indonesia: Dutch New Guinea, Sansapor Vogelkop (0°29′S, 132°05′E) [1♂, 1♀, ASM 6990–6991]; Irian Jaya (Dutch New Guinea), Schouten Island Group, Owi Island (1°15′S, 136°12′E) [2♂♂, 1 sex ?, ASM 6994, 6996–97].

Rattus feliceus Thomas, 1920 (2).—Indonesia: Maluku Province; Seram, South Coast, Piliana Village (3°15′S, 129°30′E) [1♂, 1♀, AMS 30807–808].

Rattus giluwensis (24).—Papua New Guinea: Enga Province; Porgera area, Waili Creek [1♀, 23 sex?, AMS 37998, 37998–39116].

Rattus jobiensis (5).—Indonesia: Irian Jaya (Dutch New Guinea) Schouten Island Group, Owi Island (1°15′S, 136°12′E) [1♂, 1♀, AMS 6992–93]; Irian Jaya, Supiori Island, vicinity of Kampong Korido (0°50′S, 135°36′E) [1♂, 1♀, AMS 28691–92]; Papua; Japen Island [1♂, AMNH 222435].

Rattus leucopus (60).—Indonesia: Irian Jaya, Timika area, Namco Camp, Pt. Freeport Indonesia Company (4°47′S, 136°32′E) [1♀, AMS 31671]; Irian Jaya; Timika area, Forest at New Town Complex (4°47′S, 136°32′E) [1♂, AMS 131672]; I Irian Jaya, Etna Bay vicinity of Exploration Camp [2♀♀, AMS 37370, 32373]; Maluku Province, Aru Islands, near Namara (6°03′S, 134°22′E) [5 sex?, 45592–96]. Papua New Guinea: Imanaturu Mt. Lamington District N Div. of Papua (8°50′S, 148°08′E) [1♂, 1♀, AMS 4547, 4711]; Bulolo Morobe Division (7°12′S, 146°39′E) [6♂♂, 3♀♀, AMS 6414–6422]; Dobodura, Northern Province (8°46′S, 148°23′E) [4♂♂, 2♀♀, AMS 6917, 6960, 6973–74, 6987–88]; Oriomo R W Div. Papua (9°03′S, 143°11′E) [1♂, 1♀, AMS 7237–7238]; Motu Motu Village, Brown River [1♀, AMS 7959]; South Simbu Province, Haia Vill Pio–Tura Region (6°41′S, 145°00′E) [6♂♂, 3♀♀, AMS 13836, 13838–39, 13842, 13842, 13846–13849, 13917, 13920, 13931, 13934–35, 14685–87, 14689, 14733, 14736–37, 14739, 14741, 14743, 14810, 14826, 14829, 14850–51]; Southern Highlands Province, Waro Village (6°32′S, 143°11′E) [6♂♂, 7♀♀, 2 sex?, AMS 14868, 16280–16294]; Ioma Nth Prov. (8°22′S, 147°49′E) [1♀, AMS 16325]; Sth Highland Prov, Waro (6°32′S, 143°11′E) [1♂, AMS 17128]; Central Province; Port Moresby, Laloki [1 sex?, AMS 18862]; Central Province; Dry Forest Belt 500 m Goldie River Rd (9°21′S, 147°30′E) [1♀, AMS 21695]; Southern Highlands Province, Mt. Sisa, Bobole Village (6°12′S, 142°46′E) [1♂, AMS 24291]; Southern Highlands Province; Waro Village (6°32′S, 143°11′E) [1♀, AMS 24988]; Central Province, Goldie River Road (9°21′S, 147°30′E) [1♀, AMS 26268].

Rattus mordax (29).—Papua New Guinea: Mt. Lamington Dist., Div. of Papua (8°50′S, 148°08′E) [1♀, AMS M4292); Milne Bay Province, Normanby Island, Wamla village near Guleguleu [10°30′S, 151°17′E] (3♀♀, AMS 20388–89, 20440); Fergusson Island, Kalo-kalo Village (9°25′S, 150°26′E) [11♂, AMS 28004]; German New Guinea [2 sex?, AMS 1958–59]; Dobodura North Division (8°46′S, 148°23′E) [4♂♂, 2♀♀, AMS 6913–16, 6977, 7087]; Mt. Lamington Distr. N Div. Papua (8°50′S, 148°08′E) [2♂♂, 4♀♀, AMS 4292–4293, 4685–87, 4712].

Rattus mordax mordax (1).—Papua New Guinea: Milne Bay, Gwariu River, 1 mi S of Biniguni [1♂, AMNH 158036].

Rattus praetor coenorum (15).—Indonesia: Irian Jaya (2 sex unknown, AMNH 143836–143837]; Irian Jaya; The Gebroeder Weyland Range, Mt. Derimapa [1♀, AMNH 101964]; Papua; Hollandia (now Jayapura) [1♂, AMNH 110126], Bernhard Camp, 75 m [1♂, AMNH 152356], 4 km SW Bernhard Camp, 850 m (1♀, AMNH 152358], 6 km SW Bernhard Camp, 1,200 m [1♂, AMNH 152359]; West Papua; Sansapor [1♂, USNM 277303], NW Geelvink Bay [now Cenderawasih Bay], Oransbari, el. 10′ [2 ♂♂, AMNH 222432–33], Vogelkop [1♂, AMNH 143868], Vogelkop, Sapsapore [= Sausapor?] [3♂♂, 1♀, AMNH 143843, 143849, 143851, 143871].

Rattus sanila (25).—Papua New Guinea: New Ireland Province; New Ireland Island, Balof 2 site; left maxillary fragment with M1–3 [AMS F82021—holotype], 7 maxillary and 17 right dentary fragments.

SI 2

Taxon, catalog number, collection depository, locality where collected, and GenBank voucher numbers for sequences used in phylogenetic analyses. Collection acronyms are as follows: AMS = Australian Museum; KCR = Kevin C. Rowe, personal collection, Museum Victoria; SAMA = South Australian Museum; SCU = Southern Cross University, Lismore; WAM = Western Australian Museum. Acronyms for states are as follows: NSW = New South Wales; NT = Northern Territory; QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; and WA = Western Australia; and for countries, PNG = Papua New Guinea. *CR* = mitochondrial *control region*; *ATP5A1*, *DHFR*, and *FGB*3 are nuclear genes as discussed in the Methods. Rowe et al. (2011) provide phylogenetic relationships, sequences, and data on vouchers using many, but not all, of the specimens listed here. Data for new specimens incorporated herein are provided in the Specimens Examined. Rowe et al. (2011) provide phylogenetic relationships, sequences, and data on vouchers using many, but not all, of the specimens incorporated here.

Taxon	Specimen no.	Collection	Locality	State	Country	Latitude	Longitude	*CR*	*ATP5A1*	*DHFR*	*FGB3*
Rattus colletti Thomas, 1904c	ABTC51642	SAMA	Berrimah	NT	Australia	−12.433	130.916	HQ334470	HQ334345	HQ334788	—
Rattus colletti	ABTC51650	SAMA	Fogg Dam	NT	Australia	−12.566	131.3	HQ334471	HQ334346	HQ334789	HQ334852
Rattus colletti	ABTC51656	SAMA	Humpty Doo	NT	Australia	−12.616	131.25	—	HQ334347	HQ334790	HQ334853
Rattus detentus	ABTC125036	SAMA	Kawaliap	Manus	PNG	−2.1	147.06	KP702212	KP702211	KP702218	KP702213
Rattus fuscipes assimilis (Gould, 1858)	RfaN01	KCR	Byfield National Park	QLD	Australia	−22.870	150.690	HQ334494	HQ334370	HQ334811	HQ334875
Rattus fuscipes assimilis	RfaN02	KCR	Byfield National Park	QLD	Australia	−22.838	150.669	HQ334495	HQ334371	HQ334812	HQ334876
Rattus fuscipes assimilis	RfaN05	KCR	Byfield National Park	QLD	Australia	−22.838	150.669	HQ334496	HQ334372	HQ334813	HQ334877
Rattus fuscipes	A10	SCU	Mount Nullum	NSW	Australia	−28.374	153.366	HQ334446	HQ334326	HQ334767	HQ334828

assimilis			Nature Reserve								
Rattus fuscipes assimilis	C21	SCU	Rummery Park	NSW	Australia	−28.599	153.3783	HQ334482	HQ334359	HQ334799	—
Rattus fuscipes assimilis	RfaS01	KCR	Wilson's Promontory National Park	VIC	Australia	−39.017	146.308	HQ334502	HQ334376	HQ334818	HQ334883
Rattus fuscipes assimilis	RfaS05	KCR	Wilson's Promontory National Park	VIC	Australia	−39.017	146.308	HQ334503	HQ334377	HQ334819	HQ334884
Rattus fuscipes assimilis	RfaS17	KCR	Wilson's Promontory National Park	VIC	Australia	−39.017	146.308	HQ334504	HQ334378	—	—
Rattus fuscipes coracius Thomas, 1923	DC02R06	KCR	Davies Creek State Forest	QLD	Australia	−17.039	145.614	HQ334486	—	HQ334803	HQ334867
Rattus fuscipes coracius	DC08R05	KCR	Davies Creek State Forest	QLD	Australia	−17.039	145.614	HQ334488	HQ334364	HQ334805	HQ334869
Rattus fuscipes coracius	GI02R01	KCR	Girringun National Park	QLD	Australia	−18.602	145.812	HQ334492	HQ334368	HQ334809	HQ334873
Rattus fuscipes coracius	Laurance1618	SCU	Mt. Windsor	QLD	Australia	−16.21	144.98	HQ334445	HQ334325	HQ334766	HQ334827
Rattus fuscipes coracius	PR06R01	KCR	Paluma Range National Park	QLD	Australia	−18.990	146.168	HQ334498	HQ334374	HQ334814	HQ334879
Rattus fuscipes coracius	WO04R04	KCR	Wooroonooran National Park	QLD	Australia	−17.646	145.731	HQ334506	HQ334380	HQ334824	HQ334885
Rattus fuscipes coracius	WO04R06	KCR	Wooroonooran National Park	QLD	Australia	−17.646	145.731	HQ334508	HQ334382	HQ334822	HQ334887
Rattus fuscipes coracius	WO05R04	KCR	Wooroonooran National Park	QLD	Australia	−17.656	145.714	HQ334510	HQ334384	HQ334824	HQ334889
Rattus fuscipes	WO05R11	KCR	Wooroonooran	QLD	Australia	−17.656	145.714	HQ334512	HQ334386	HQ334826	HQ334891

coracius			National Park								
Rattus fuscipes fuscipes	ABTC08616	SAMA	26 km W Manjimup	WA	Australia	−34.25	116.033	HQ334450	HQ334330	HQ334771	HQ334832
Rattus fuscipes fuscipes	ABTC08644	SAMA	Greenhead	WA	Australia	−30.067	114.967	HQ334451	HQ334331	HQ334772	HQ334833
Rattus fuscipes greyi (Gray, 1841)	RAT60	SCU	Scott Creek	SA	Australia	−34.933	138.667	HQ334501	HQ334375	HQ334817	HQ334882
Rattus giluwensis	ABTC87301	SAMA	Waile Creek Porgera	Enga	PNG	−5.547	143.073	HQ334478	HQ334355	HQ334796	HQ334861
Rattus giluwensis	ABTC87305	SAMA	Waile Creek Porgera	Enga	PNG	−5.547	143.073	HQ334479	HQ334356	HQ334795	HQ334862
Rattus leucopus cooktownensis Tate, 1951	ABTC51770	SAMA	Home Rule	QLD	Australia	−15.75	145.283	HQ334477	HQ334354	HQ334804	HQ334860
Rattus leucopus cooktownensis	DC07R02	KCR	Davies Creek State Forest	QLD	Australia	−17.037	145.61	HQ334487	HQ334363	HQ334806	HQ334868
Rattus leucopus cooktownensis	DC11R05	KCR	Dinden National Park	QLD	Australia	−16.980	145.70	HQ334489	HQ334365	HQ334807	HQ334870
Rattus leucopus cooktownensis	DT01R03	KCR	Daintree National Park	QLD	Australia	−16.474	145.327	HQ334490	HQ334366	HQ334808	HQ334871
Rattus leucopus cooktownensis	DT10R02	KCR	Daintree National Park	QLD	Australia	−16.042	145.459	HQ334491	HQ334367	HQ334817	HQ334872
Rattus leucopus cooktownensis	PR04R01	KCR	Paluma Range National Park	QLD	Australia	−18.862	146.116	HQ334497	HQ334373	—	HQ334878
Rattus leucopus cooktownensis	WO04R05	KCR	Wooroonooran National Park	QLD	Australia	−17.646	145.731	HQ334507	HQ334381	HQ334821	HQ334886
Rattus leucopus cooktownensis	WO04R09	KCR	Wooroonooran National Park	QLD	Australia	−17.646	145.731	HQ334509	HQ334383	HQ334823	HQ334888
Rattus leucopus cooktownensis	WO05R09	KCR	Wooroonooran National Park	QLD	Australia	−17.656	145.714	HQ334511	HQ334385	HQ334825	HQ334890

Rattus leucopus dobodurae Troughton, 1946	M14739	AMS	Haia	Chimbu	PNG	−6.683	145	—	—	HQ334774	HQ334836
Rattus leucopus dobodurae	M14741	AMS	Haia	Chimbu	PNG	−6.683	145	HQ334454	—	HQ334775	HQ334837
Rattus leucopus dobodurae	M13838	AMS	Haia	Chimbu	PNG	−6.683	145	HQ334455	HQ334333	HQ334776	HQ334838
Rattus leucopus dobodurae	M14743	AMS	Haia	Chimbu	PNG	−6.683	145	HQ334456	HQ334334	HQ334777	HQ334839
Rattus leucopus dobodurae	M13931	AMS	Haia	Chimbu	PNG	−6.683	145	HQ334457	HQ334335	HQ334778	HQ334840
Rattus leucopus dobodurae	M13849	AMS	Haia	Chimbu	PNG	−6.683	145	HQ334480	HQ334357	HQ334797	HQ334863
Rattus leucopus leucopus	ABTC08493	SAMA	Rocky River	QLD	Australia	−13.783	143.533	HQ334449	HQ334329	HQ334770	HQ334831
Rattus leucopus leucopus	IR02R02	KCR	Iron Range National Park	QLD	Australia	−12.674	143.334	HQ334493	HQ334369	HQ334810	HQ334874
Rattus leucopus leucopus	SP03R01	KCR	Silver Plains Homestead	QLD	Australia	−13.834	143.452	HQ334505	HQ334379	HQ334820	—
Rattus leucopus ringens (Peters and Doria, 1881)	M16281	AMS	Waro	Southern Highlands	PNG	−6.533	143.183	HQ334461	HQ334337	—	HQ334844
Rattus leucopus ringens	M17128	AMS	Waro	Southern Highlands	PNG	−6.5	143	HQ334481	HQ334358	HQ334798	HQ334864
Rattus lutreolus lutreolus (Gray, 1841)	D39	SCU	Tyagarah	NSW	Australia	−28.59	153.55	HQ334483	HQ334360	HQ334800	HQ334865
Rattus lutreolus lutreolus	ABTC51720	SAMA	Myall Lakes	NSW	Australia	−32.433	152.367	HQ334475	HQ334352	HQ334793	HQ334858
Rattus lutreolus velutinus (Thomas,	D69	SCU	Hobart	TAS	Australia	−42.883	147.31	HQ334485	HQ334362	HQ334802	—

1882)											
Rattus lutreolus velutinus	ABTC51762	SAMA	Derwent Valley	TAS	Australia	−41.317	148.1	HQ334476	HQ334353	HQ334794	HQ334859
Rattus mordax	M27993	AMS	Woodlark Island	Milne Bay	PNG	−9.216	152.933	KP702214	—	—	—
Rattus mordax	M27993	AMS	Fergusson Island	Milne Bay	PNG	−9.416	150.433	KP702216	KP702219	KP702220	KP702217
Rattus niobe	M12872	AMS	Mt. Albert Edward	Central	PNG	−8	147	HQ334453	HQ334332	HQ334773	HQ334835
Rattus niobe	M16311	AMS	near Apia River	Southern Highlands	PNG	−6.15	142.767	HQ334459	HQ334336	HQ334780	HQ334842
Rattus niobe	M17664	AMS	Sol River	Sandaun	PNG	−5.15	141.633	HQ334464	—	HQ334784	HQ334847
Rattus novaeguineae Taylor and Calaby 1982	M14647	AMS	Yuro	Southern Highlands	PNG	−6.533	144.85	HQ334458	—	HQ334779	HQ334841
Rattus novaeguineae	M16318	AMS	Waro	Southern Highlands	PNG	−6.533	143.183	HQ334460	—	HQ334781	HQ334843
Rattus novaeguineae	M19055	AMS	Nokopo	Morobe	PNG	−5.95	146.6	HQ334468	HQ334343	—	HQ334850
Rattus novaeguineae	M19056	AMS	Nokopo	Morobe	PNG	−5.95	146.6	HQ334469	HQ334344	—	HQ334851
Rattus praetor	M17484	AMS	Munbil	Sandaun	PNG	−4.867	141.217	HQ334465	HQ334340	HQ334785	HQ334848
Rattus praetor	M17461	AMS	Munbil	Sandaun	PNG	−4.867	141.217	HQ334466	HQ334341	HQ334786	—
Rattus praetor	M17459	AMS	Munbil	Sandaun	PNG	−4.867	141.217	HQ334467	HQ334342	HQ334787	HQ334849
Rattus rattus	A65	SCU	Nymboida	NSW	Australia	−30.35	152.48	HQ334447	HQ334327	HQ334768	HQ334829
Rattus sordidus (Gould, 1858)	RAT176	SCU	Innisfail	QLD	Australia	−17.517	146.017	HQ334500	—	HQ334791	HQ334881
Rattus sordidus	ABTC51664	SAMA	Ingham	QLD	Australia	−18.65	146.15	HQ334472	HQ334348	HQ334816	HQ334854
Rattus steini	M17691	AMS	Sol River	Sandaun	PNG	−5.15	141.633	HQ334462	HQ334338	HQ334782	HQ334845
Rattus tunneyi culmorum (Thomas and Dollman, 1909)	D45	SCU	Bundjalong National Park	NSW	Australia	−29.333	153.433	HQ334484	HQ334361	HQ334801	HQ334866

Rattus tunneyi culmorum	RAT132	SCU	Yarraman	QLD	Australia	−26.833	151.983	HQ334499	—	HQ334815	HQ334880
Rattus tunneyi tunneyi (Thomas, 1904b)	M21990	WAM	Mitchell Plateau	WA	Australia	−14.767	125.783	HQ334452	—	—	HQ334834
Rattus tunneyi tunneyi	ABTC51684	SAMA	Edward Pellew Island	NT	Australia	−15.5	136.75	HQ334474	HQ334351	HQ334792	HQ334857
Rattus verecundus (Thomas, 1904c)	M17628	AMS	Sol River	Sandaun	PNG	−5.15	141.633	HQ334463	HQ334339	HQ334783	HQ334846
Rattus villosissimus (Waite, 1898)	ABTC08439	SAMA	Midway Tank	QLD	Australia	−24.633	140.95	HQ334448	HQ334328	HQ334769	HQ334830
Rattus villosissimus	ABTC51675	SAMA	Perikoola Water Hole	QLD	Australia	−25.683	140.6	HQ334473	HQ334350	—	HQ334856

S3

Measurements of specimens of *Rattus detentus* from the Pamwak archaeological site, deposited at PNGMAG. Specimens are identified by Excavation Square (Squ), Quadrant (Quad), and Spit (vertical excavation unit) (see Fredericksen et al. 1993). Isolated lower and upper incisors of *R. detentus* are distinguished from those of *Melomys matambuai* by a combination of their larger size, more extensively enameled medial surface (enamel extends at least 0.5 mm onto the medal surface vs. no more than 0.3 mm in *M. matambuai*), and presence of a beveled rather than rounded intersection between the anterior and lateral surfaces of the tooth.

Table 1. Measurements of the lower dentition and mandibular ramus. Measurements are m1–3 crown length (CL), m1–3 alveolar length (AlvL), m1 crown length (CL), m1 crown width (CW), m2 crown length (CL), m2 crown width (CW), m3 crown length (CL), m3 crown width (CW), lower incisor depth (Lower I D), lower incisor width (Lower I W). Incisor depth is the least distance from the most proximal point on the occlusal facet to the opposite side (termed "antero-posterior diameter" and diagrammed by Millien-Parra and Loreau 2000).

Squ	Quad	Spit	m1–3 CL	m1–3 AlvL	m1 CL	m1 CW	m2 CL	m2 CW	m3 CL	m3 CW	Lower I D	Lower I W
4	NW	12B	8.25	8.45	3.15	2.1	2.25		2.65	2.05		
4	N	2B		8.75	3.15	2	2.45	2.35			2.65	1.4
4	NW	2B			3.15	2	2.45	2.25			2.6	1.6
2	S	11B			3.15	2	2.5	2.2			2.55	
4	NEQ	3A			3.15	1.9					2.7	1.4
4	NW	2C	7.7	7.9	3.2	2.05	2.2	2.2	2.25	1.7		
2	S	4A		8.9	3.2	2.1	2.2	2.45	2.55	2.1		
2	STLC	4B			3.2	2.15	2.45	2.4			2.55	1.4

4	NEQ	2C		8.9	3.25	2.05						1.5
4	SW	3B	8.25	8.3	3.3	2.05	2.3	2.25	2.5	1.85		
4	SW	2B		8.75	3.3	2.1	2.4	2.5			3	1.6
2	NW	10A			3.3	2.15	2.5	2.5				
3	SEQ	3B			3.35	2.15	2.4	2.35			2.55	1.55
2	MS/WA	3	8.45	8.85	3.35	2.35	2.45	2.45	2.4	2.05		
2	MS/WA	3		8.55	3.35	2.15	2.45	2.35				
2	N	5A			3.35	2.15	2.5	2.4	2.65	2		
2	S	5B			3.35	2.1	2.5	2.3				
2	NQ	4A			3.35	2	2.6	2.25				
4	S	3A		8.95	3.4	2.15	2.35	2.4		2	2.95	1.6
2	MS/WA	4			3.4	2.1	2.5	2.3	2.4	1.9	2.75	1.5
4	SW	3B		8.5	3.4	2.15	2.55	2.25	2.15	2		
4	N	3A		8.4	3.45	2.25	2.5	2.5				1.35
4	NEQ	2B		9.05	3.5	2.1	2.45	2.35			2.85	1.6
4	SW	2A		8.35	3.5	2.1	2.5	2.4	2.4	1.85		
3	NW	5B	8.5	8.85	3.5	2.15	2.5	2.45	2.45	2.05		
2	SEQ	7B		8.9	3.5	2.15	2.5	2.4	2.45	2.1	2.85	1.65
4	NW	2B			3.5	2.15					2.6	1.8
4	NEQ	1		9.3	3.75	2.4	2.65	2.6	2.55	2.25	3	1.8
2	MS/WA	4					2.55	2.4				
2	S	3A		9			2.6	2.5	2.5			
4	S	7B						2.4			2.7	1.6
2	MS/WA	4		7.55								
2	SEQ	16A		8.75								1.3
2	SW	10A		9								
4	SEQ	2C		9.3								1.9
2	N	10A									2.4	1.3
2	S	10A									2.45	1.35
2	NW	10A									2.15	1.2
2	NW	10A									2.65	1.5
2	SEQ	10B									2.55	1.6
2	S	11A									2.65	1.55
2	NEQ	11A									2.5	1.45

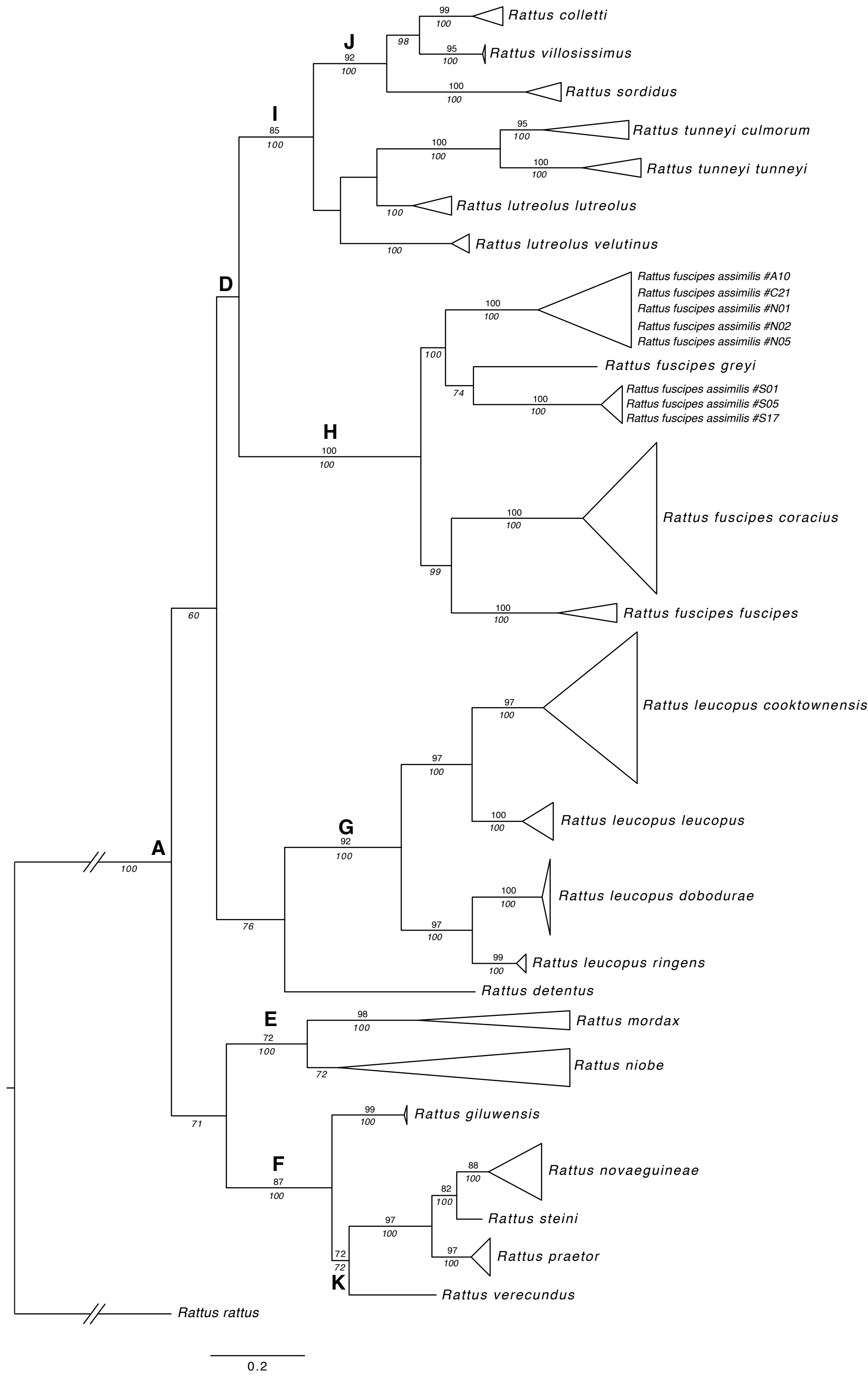
2	N	11A	2.8	1.5
4	S	11A	2.35	1.4
2	S	11B	2.35	1.25
2	N	12B	2.65	1.6
2	SEQ	13A	2.5	1.5
2	SEQ	13B	2.65	1.45
2	NEQ	13B	2.65	1.55
4	SW	13B	2.4	1.35
2	SW	14A	2.5	1.4
2	NEQ	14A	2.3	1.3
2	NEQ	14A	2.2	1.3
4	SW	14A	2.4	1.4
2	SW	14B	2.45	1.4
2	S	15A	2.55	1.4
2	SEQ	16B	2.05	1.25
1	NEQ	21B	2.4	1.4
1	NEQ	22A	2.45	1.45
1	NEQ	22A	2.2	1.35
1	SEQ	24A	2.35	1.45
4	NW	2B	2.2	1.45
4	NW	2B	3.2	1.8
4	NW	2C	2.7	1.5
3	SEQ	2D	2.1	1.2
4	NW	2D	2.15	1.2
4	N	3A	3.05	2.1
4	N	3A	2.7	1.4
2	S	3B	2.45	1.05
4	NW	3B	2.3	1.25
4	NW	3B	2	1.2
4	NW	3B	2.4	1.25
4	NEQ	4A	3	1.6
2	N	4B	2.5	1.6
4	NW	4B	2.5	1.35
4	NW	4B	2.45	1.6

2	NW	5A		1.6
4	SEQ	5A	2.4	1.2
4	NW	5A	2.35	1.45
4	N	5A	2.7	1.55
2	N	5B	2.9	1.7
2	S	5B	2.9	1.5
2	NW	6A	2.7	1.55
2	NW	6A	2.05	1.15
3	NEQ	6A	2.35	1.2
3	NEQ	6A	2.45	1.3
2	NW	7A	2.6	1.3
2	NW	7A	2.35	1.5
2	S	7A	2.65	1.5
3	SEQ	7A	3.25	1.75
4	SW	7A	2.5	1.55
4	NW	7A	2.7	1.5
4	N	7A	2.35	1.25
2	NW	7B	2.45	1.35
2	NW	7B	2.65	1.55
4	S	8A	2.1	1.1
2	N	8B	2.05	1.35
4	S	8B	2.35	1.3
2	SW	9A	2.4	1.35
2	SEQ	9B	2.7	1.45
2	SW	9B	2.6	1.35

Table 2. Measurements of the upper dentition and maxilla. Measurements are M1–3 alveolar length (M1–3 Alv L), M1 crown length (M1 CL), M1 crown width (M1 CW), zygomatic plate width (Zyg Pl W), upper incisor depth (Upper I D), upper incisor width (Upper I W).

Squ	Quad	Spit	M1–3 Alv L	M1 CL	M1 CW	Zyg Pl W	Upper I D	Upper I W
2	MS/WA	4				5.7		
2	NW	8B	9					
4	NW	2A		4.2	2.65			
4	S	4A			2.5			
3	NE	5A		4.2	2.45			
4	SW	20					3.35	1.8
2	NW	10B					3.1	1.7
2	SW	11A					3.25	1.7
2	N	12A					3.1	1.7
2	SEQ	13B					3.05	1.55
4	SW	13B					3.25	1.7
2	SW	14B					2.9	1.65
2	NW	15B					3.25	2
1	SEQ	21B					2.7	1.6
1	SEQ	21B					2.3	1.35
1	SEQ	27A					3.1	1.75
1	NEQ	28A					2.65	1.7
2	S	2B					3.1	1.7
4	SW	2B					3.1	1.7
4	NEQ	2B					3.4	1.95
4	NEQ	3A					3.05	1.65
4	SEQ	3A					3.25	1.9
2	S	3B					2.85	1.45
4	SW	3B					3.35	1.9
4	N	3B					3.2	1.85
2	S	4A					3.65	2.05
4	NEQ	4B					3.6	1.8
4	NW	4B					2.9	1.7
2	S	5A					3.5	1.95
2	N	5A					3.15	1.85
3	NEQ	5A					3.25	1.85

4	N	5A		3.1	1.75
4	SW	5A		3.4	1.9
2	S	5B		3.45	1.8
3	SEQ	6A		3.15	1.8
4	N	6A		3.05	1.65
2	N	7B		3.1	2.05
4	N	8A		3.55	2.1
2	N	9B		3	1.7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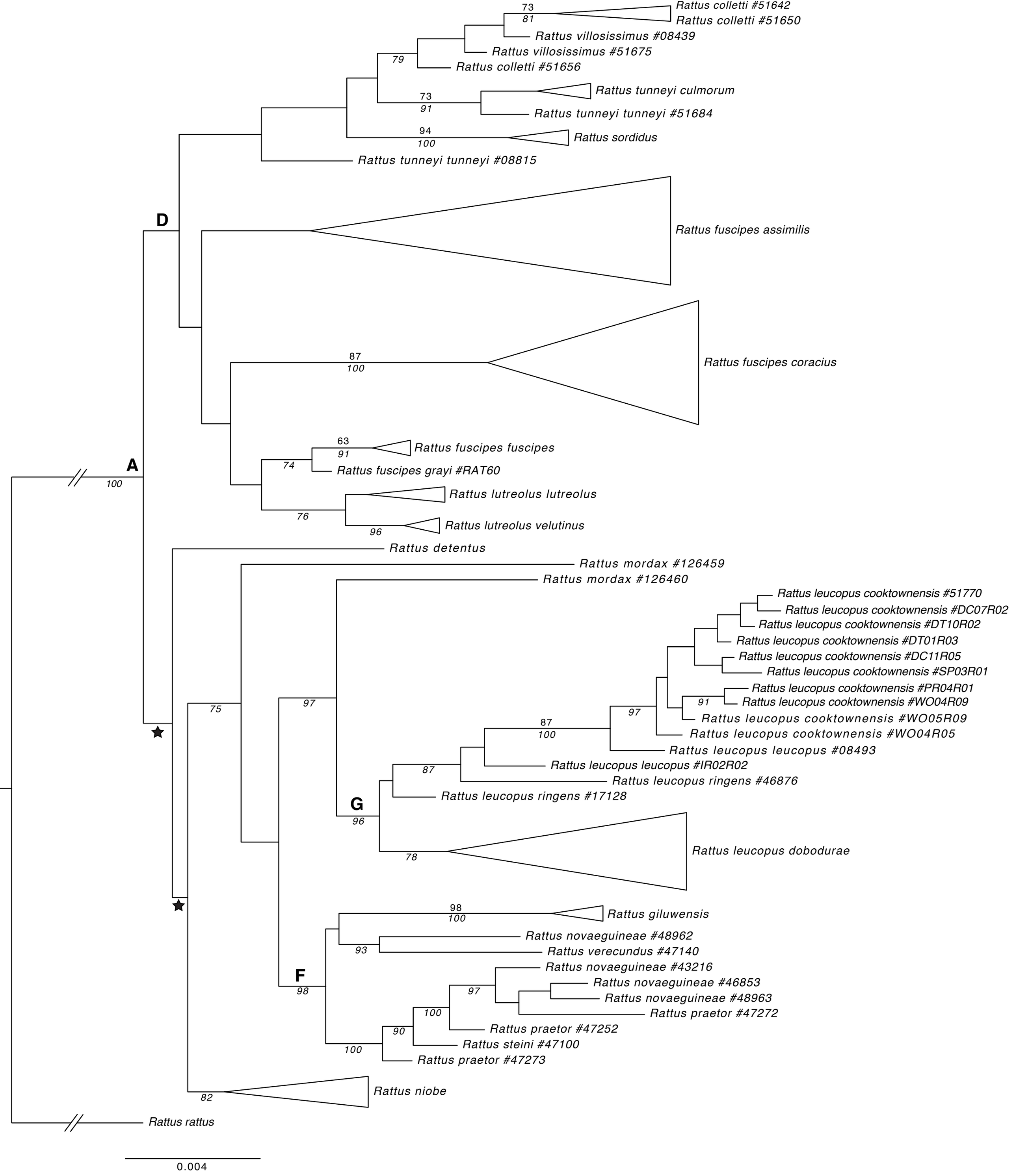
Rattus sordidus
Rattus tunneyi culmorum
Rattus tunneyi tunneyi
Rattus lutreolus lutreolus
Rattus lutreolus velutinus
Rattus fuscipes assimilis #A10
Rattus fuscipes assimilis #C21
Rattus fuscipes assimilis #N01
Rattus fuscipes assimilis #N02
Rattus fuscipes assimilis #N05
Rattus fuscipes greyi
Rattus fuscipes assimilis #S01
Rattus fuscipes assimilis #S05
Rattus fuscipes assimilis #S17
Rattus fuscipes coracius
Rattus fuscipes fuscipes
Rattus leucopus cooktownensis
Rattus leucopus leucopus
Rattus leucopus dobodurae
Rattus leucopus ringens
Rattus detentus
Rattus mordax
Rattus niobe
Rattus giluwensis
Rattus novaeguineae
Rattus steini
Rattus praetor
Rattus verecundus
Rattus rattus
A
D
H
I
J
G
E
F
K
0.2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Rattus colletti #51650
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Rattus villosissimus #51675
Rattus colletti #51656
Rattus tunneyi culmorum
Rattus tunneyi tunneyi #51684
Rattus sordidus
Rattus tunneyi tunneyi #08815
D
Rattus fuscipes assimilis
Rattus fuscipes coracius
Rattus fuscipes fuscipes
Rattus fuscipes grayi #RAT60
A
Rattus lutreolus lutreolus
Rattus lutreolus velutinus
Rattus detentus
Rattus mordax #126459
Rattus mordax #126460
Rattus leucopus cooktownensis #51770
Rattus leucopus cooktownensis #DC07R02
Rattus leucopus cooktownensis #DT10R02
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Rattus leucopus leucopus #08493
Rattus leucopus leucopus #IR02R02
Rattus leucopus ringens #46876
Rattus leucopus ringens #17128
G
Rattus leucopus dobodurae
Rattus giluwensis
Rattus novaeguineae #48962
Rattus verecundus #47140
Rattus novaeguineae #43216
Rattus novaeguineae #46853
Rattus novaeguineae #48963
Rattus praetor #47272
Rattus praetor #47252
Rattus steini #47100
Rattus praetor #47273
F
Rattus niobe
Rattus rattus
0.004